Fall 12-16-2016

Phylogenetics, biogeography, and climate niche variation of South Pacific and Hawaiian Psychotria

Elaine Zhang
elazhang888@gmail.com

Phylogenetics, biogeography, and climate niche variation of South Pacific and Hawaiian *Psychotria*

by

Elaine Zhang

Thesis
Submitted in Partial Satisfaction of the Requirements
For the Degree of

Masters of Science
In Biology

In the
College of Arts & Sciences
University of San Francisco
San Francisco, California
2017

Committee in Charge

John R. Paul
James Sikes
Scott Nunes

ABSTRACT

Why do some species have broad geographic distributions, while other species are confined to a narrow distribution? Species age, ecological niche, or dispersal traits may help explain why some insular species are abundant and found on many islands, while others are rare and restricted to one island. In this study, I inferred a robust, time-calibrated phylogeny of the Hawaiian *Psychotria*, using two nuclear and eight chloroplast loci, sampling 67 individuals. I coupled my phylogenetic hypothesis with climatic data, ecological niche modeling, and morphological dispersal characteristics to explain the variation in number of islands occupied by each species. My inferred phylogeny showed stronger support for many relationships among the Hawaiian species. Restricted lineages on the older islands were found to be basal, while younger, derived species were more widespread. The species that have managed to disperse to and colonize multiple islands are the younger species. The biogeographical South Pacific *Psychotria* suggests strong biogeographic structure, with early divergences of major clades and very few species subsequently dispersing and colonizing other geographic regions. Results of niche breadth and climatic niche models of the Hawaiian species indicate a general pattern of older species having narrower climatic niche breadths, which may explain their smaller geographic ranges. In contrast, the younger species have wider climatic niche breadths, which may explain why they occupy larger geographic ranges across multiple islands. However, multiple regression analysis indicate greater plant height (associated with dispersal abilities) has the strongest weight in explaining the number of islands Hawaiian *Psychotria* species occupy.

ACKNOWLEDGMENTS

I would like to first thank my thesis advisor, Dr. John R. Paul of the College of Arts & Sciences at University of San Francisco (USF). I cannot express enough gratitude and appreciation for all the support and opportunities he has given me. His guidance and exceptional knowledge helped steer me in the right direction at times when there were questions about the research or writing. His encouragement and belief has allowed me to push my boundaries and become a more confident scientist and researcher. He will always be a great advisor, mentor, professor, colleague, and friend. I give my sincerest thanks for everything and for the continuous support.

I would also like to thank my thesis committee: Dr. John R. Paul, Dr. Sikes, and Dr. Nunes of the College of Arts & Sciences at USF. I am grateful for all the guidance and valuable inputs they provided for thesis to be completed successfully.

This thesis project would not have been completed had it not been for the National Tropical Botanical Garden (NTBG) in Kauai for allowing herbarium sampling of *Psychotria* species. I would like to give thanks to our collaborators, Dr. David Lorence and Dr. Kenneth Wood at NTBG, and Dr. Kenta Watanabe of Okinawa National College of Technology in Okinawa, for especially curating the samples, and for being great mentors in the field during our research expedition in Kauai.

I would also like to thank the University of San Francisco Faculty Development Fund (FDF) for allowing my research to take place in the Biology Department of University of San Francisco. And thanks to the faculty and staff in the Biology Department, members of the John Paul Lab, and Dr. April Randle, with whom I got the chance to work with and got to know throughout my time in the program.

Finally, I give my deepest gratitude to my family and friends, especially to Mom and Dad. My heartfelt thanks to both of you for allowing me to pursue my education with your utmost love, support, encouragement, and much appreciated advice on life.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE **PAGE**

INTRODUCTION

Understanding the factors that regulate the abundance and distribution of organisms is a central goal of ecological research. Species vary dramatically in their absolute abundances and geographic ranges sizes (Gaston 2003). Much of this variation is expected, given the unique ecological niches, specialized habitats, and ways of making a living that organisms possess. However, even closely-related species that are remarkably similar in their attributes can vary greatly in their abundance and distribution (Gaston 2003; Paul et al. 2009).

What factors are most important in driving the variation in abundance and distribution of closely-related species? This is a complicated and multifaceted question that likely has many answers depending on the lineages that are studied. Explaining variation in abundance has traditionally been the purview of ecological studies focusing on proximate causes (Ricklefs 2008). In local communities, competition, predation, herbivory, and mutualistic interactions have all been shown to be important drivers of variation in abundance (Ricklefs 1987). When taking a more regional perspective, variation in the distribution of organisms can be viewed by contrasting their geographic range sizes.

Only more recently have studies started to explicitly incorporate an evolutionary perspective (Paul et al. 2009) on variation in abundance and distribution. Evolutionary history has been proposed to be important in particular to explain variation in distributions as quantified through geographic range sizes (Swaegers et al. 2014). A number of general hypotheses have been

proposed to explain variation in range size of closely-related species. First, species age was proposed to be important to geographic range size in the 1920s by John Willis (Willis 1922), whose 'age-and-area hypothesis' predicted many species with small geographic ranges are simply evolutionarily young species. Recently, some empirical evidence has been found for this pattern (Paul et al. 2009), but other studies have found no relationship between species age and range size (Jones et al. 2005). Further, Pigot et al. (2012) used simulations to argue that directional range size evolution patterns are mainly an artifact of the processes of speciation and extinction. Conversely, others have proposed that many species with restricted geographic ranges are 'relict species' – species that once had larger ranges but have failed to adapt to changing climatic conditions (Murray & Hose 2005). The California redwoods and sequoias have been proposed as such lineages (Florin 1963), as their clade once had a much broader global distribution. However, Ricklefs (2012) argued that overall species age shows little consistent relationship with range size and hence is a weak predictor.

If species age alone can't explain range size variation, it doesn't lessen the importance of an evolutionary perspective, as species inherit their characteristics from their ancestors, and lineages may vary in how quickly characteristics evolve. Of particular interest to geographic ranges is the ecological niche, which can be defined as the set of ecological conditions in which a given species can maintain stable or positive population growth (Angert 2009). Variation in ecological niches, and by extension, the ecological tolerances of species, should be critical in determining where a species can successfully survive. Furthermore, geographic ranges can be viewed as

spatial manifestations of the ecological niche (Pulliam 2000), and as such, provide a means to quantify and compare the ecological niches of species.

The relationship between ecological niches and geographic ranges has been examined through lens of niche breadth, the range of environmental conditions a species can tolerate, and niche lability, the ability of a lineage to transform its ecological niche characteristics over time. Species with broader ecological niches may be expected to have larger geographic ranges (Slayter et al. 2013; Sheth & Angert 2014), simply because these species can occupy a greater proportion of ecological niche space distributed in the environment. As a corollary, species with narrow niche breadths that can only tolerate a limited set of ecological conditions are expected to have smaller geographic ranges. Of course, these predicted patterns can be easily thrown into array, if for example, a particular habitat that a species with a narrow niche breadth specializes on is abundant and widespread across the landscape. Empirical evidence for the relationship between niche breadth and range size is somewhat sparse, but recent research has been support (Sheth & Angert 2014) and some argue for the generality of this relationship (Slayter et al. 2013).

How quickly a lineage or species' ecological niche evolves may also have an impact on geographic distributions. Similar to a species with a broad ecological niche, a species that can evolve its ecological niche characteristics quickly may also rapidly transform its geographic range size. Such niche labile lineages can be exemplified through adaptive radiations – rapid diversification and niche expansion via adaptive evolution (Givnish et al. 2009). The Hawaiian silverswords, plants in family Asteraceae, provide a classic example of adaptive radiations.

Phylogenetic analysis of the Hawaiian silverswords shows they share a common ancestor with a clade of California tarweeds, and suggest a single dispersal event less than 6 mya founded the original Hawaiian ancestral population (Baldwin et al. 1991). From there, over 50 distinct species have evolved over the course of only 5 my. Most remarkable though is the ecological and morphological variability this clade expresses, with some Hawaiian species being small seaside herbs, similar to the California tarweeds, and some being succulents, woody climbers, shrubs, and even trees. Furthermore, this clade has a very broad climatic niche with the sum of the species distributed across all islands, from sea level to over 3000 m elevation on Mauna Kea, Hawaii. In contrast, species that evolve their ecological niche characteristics slowly may fail to expand their geographic ranges over evolutionary time. Such species exemplify niche conservatism, the tendency of species to maintain the ecological niches of their ancestors (Wiens et al. 2010). Niche conservative species may also have increased difficulty maintaining species cohesion because of barriers to gene flow imposed by tracts of unsuitable habitat, leading ultimately to lineage splits in the absence of substantial ecological niche evolution (Wiens et al. 2010).

Recently, ecological niche modeling (ENM) methods have been developed to estimate a species' climatic niche characteristics using geographic distribution data (Phillips et al. 2004; Phillips et al. 2006). Specifically, this set of methods uses the geographic coordinates from collection records of a given species to extract a set of climatic variables (e.g., mean annual precipitation, mean annual temperature, etc.) from a global database (e.g., WorldClim, Hijmans et al. 2005) for those specific geographic coordinates. By integrating the climatic values across a set of

collection records, the predicted ecological niche conditions in which a species can occur is estimated, and a predicted geographic range can be extrapolated. The practicality of these methods is enhanced by the subset of methods that only requires presence points (e.g., collection records from a museum or herbarium) to estimate the niche, but requires no absence points (which are typically unknown). The utility of these methods has led to an explosion of studies incorporating ENMs to answer a wide range of questions, from conservation purposes (Raxworthy et al. 2003) to the evolution of climatic niches (Kozak and Wiens 2010; Title & Burns 2015), and the explanations of patterns of diversification and species richness (Kozak & Wiens 2010).

Dispersal by definition is required to expand a species' geographic range, so naturally variation in dispersal ability has been proposed to be an important factor (Brown et al. 1996; Iversen et al. 2013). Dispersal is the ecological process where individuals move away from their source population to novel habitats. In some cases, dispersal ability appears to be more important than ecological tolerances to predict geographic range size (Arribas et al. 2012). Yet despite the intuitive importance of dispersal characteristics, their ability to explain variation in geographic range size has been limited (Lester et al. 2007; Gove et al. 2009).

Islands provide a unique setting to examine distributions and have played an important role in ecological and evolutionary theory (Whittaker et al. 2008; Gillespie & Baldwin, 2010). Island biogeography is a theory that explains the factors and biological processes that affect species richness on oceanic islands, focusing on the roles in island size and distance from the mainland

and in rates of colonization and extinction (MacArthur & Wilson 1967). Oceanic islands provide a unique and effective model for testing geographical and ecological properties influencing endemic diversity (MacArthur & Wilson 1967). More recently, the 'General Dynamic Model of Oceanic Island Biogeography' (Whittaker et al. 2008), states diversification is greatest on larger islands that are remote, allowing for rapid diversification amongst the few lineages that manage to colonize remote islands (MacArthur & Wilson 1967). In addition, islands are often comprised of novel habitats that may promote rapid evolution of new adaptations (Bennett et al. 2013), ultimately leading to adaptive radiation. Island radiations are driven by island colonization via a founder event and subsequent genetic divergence from source populations via natural selection and genetic drift (Dixon et al. 2011). Evolutionary processes that underlie island adaptive radiations, such as how species diversify in these novel ecological niches given new resources within confined geographical regions (Schluter 2000), still remain unclear (Kapralov et al. 2013). However, key adaptive radiations on islands have been viewed to follow similar processes as on continents, thus examining islands can provide a general understanding of adaptation and the drivers of species diversity (Emerson 2002).

Colonization of islands is driven by a species' dispersal abilities (Fritz et al. 2012). Dispersal is an important factor regulating whether colonization events are successful and whether species subsequently spread across island archipelagos, ultimately influencing patterns of species distribution and abundance. If dispersal abilities are low, colonization events may lead to species divergence and possibly speciation. However, if dispersal abilities are high, gene flow can occur between islands preventing speciation (Dixon et al. 2011). Islands provide limited available

ecological niche conditions due to limited range size (Kapralov et al. 2013). Therefore, limited ecological space may restrict diversity due to decrease in genetic variability within a small population size (Dixon et al. 2011). However, steep ecological gradients can promote diversity within a small amount of ecological space, especially among species with high dispersal abilities (Frankham 1997). Islands also exhibit taxon cycles, defined as the cyclic evolution of species (Wilson 1961) where species' ranges undergo sequential phases of expansion and contraction resulting in shifts in relative distribution and abundances of species across islands (Ricklefs et al. 2002). Taxon cycles can provide understanding of distribution and extinction patterns across island chains by examining interactions between colonizing and resident species. Such interactions can give rise to gaps in island occupancy if either the novel or native species faces extinction due to genetic divergence between island populations after colonization from one island to another, thus leading to range contraction (Ricklefs et al. 2002). The causes of taxon cycles are unknown, but have thought to be driven by coevolution among novel and native species (Ricklefs et al. 2002).

In this study, I use the Hawaiian *Psychotria* diversification as a model system to understand the drivers of variation in abundance and distribution. *Psychotria* (Rubiaceae; the coffee family) is one of the most species rich genera of plants in the world (~1600 species; Paul et al. 2009) and pantropical in distribution with diversifications across various continents and islands of the South Pacific and the Caribbean (Nepokroeff et al. 2003). South Pacific islands have many endemic and very few widespread species, whereas in the Caribbean there are fewer endemics and more widespread continental species (Nepokroeff et al. 1999; Sohmer 1977; Taylor 1996). This

pantropic distribution suggests considerable dispersal abilities among species of *Psychotria*, which typically have red, blue, orange or purple fruits that are dispersed by birds. However some species within *Psychotria* have remained confined to single oceanic island (or in a continental setting, mountaintop or unique habitat island) and do not disperse across islands. Why is this the case? Species of *Psychotria* also vary tremendously in geographic range size, both generally (Paul et al. 2009) and specifically in Hawaii. *Psychotria grandiflora* and *Psychotria hobdyi*, for example, both have very small range sizes and are only found on the northwest corner of Kauai, the oldest island of the Hawaiian Islands. In contrast, *Psychotria mariniana* exhibits a relatively larger geographic range and is found distributed across multiple Hawaiian islands: Kauai, Oahu, Molokai, Lanai, and Maui (Nepokroeff et al. 2003). Why do these closely-related species vary so greatly in their distributions? Previous work has shown that some *Psychotria* species transform their ranges slowly (rare species = young species; Paul et al. 2009). This suggests species of *Psychotria* are good at dispersing over long distances over long time periods, but are slow to expand their range size in absolute time. Other recent work reveals *Psychotria* species exhibit phylogenetic niche conservatism in climatic characteristics, with the inferred climatic niches of ancestral species being a strong predictor of microhabitat associations in Neotropical species, even after millions of years of divergence and dispersal (Sedio et al. 2013). Do Hawaiian *Psychotria* display similar evidence of conservatism in climatic niche traits? Do species that inhabit many islands occupy similar or different climatic niche space on different islands? And are species that have colonized multiple islands also those with the greatest climatic niche breadth?

Hawaiian *Psychotria* are a relatively small radiation with 11 recognized species and numerous named subspecies and/or varieties (Nepokroeff et al. 2003) that provide a textbook example of older-to-younger island colonization (see Fig. 6.11 in Futuyma 2013). In previous phylogenetic work, Nepokroeff et al. (2003) used two nuclear ribosomal DNA markers (ITS and ETS) to build the first phylogeny of Hawaiian *Psychotria* species relationships. This pioneering work laid the groundwork for future work in Hawaiian *Psychotria.* However, one obvious limitation of this study was the use of only two loci, both of which are ribosomal nuclear markers. As a result, they found low support for the inferred relationships between some of the younger Hawaiian species (Nepokroeff et al. 2003). In addition, this study did not incorporate any chloroplast markers, yet some chloroplast markers can be useful for species-level discrimination, particularly when paired with nuclear markers such as ITS (China Plant BOL Group et al. 2011). Nepokroeff et al. (2003) also sequenced relatively few samples for a given species, and their results point to some species with multiple accessions as non-monophyletic, especially when the same putative species was sampled on different islands. This calls for more collections of individuals per species as well as using additional nuclear and chloroplast markers to develop a robust phylogeny of Hawaiian *Psychotria* in order to resolve these relationships. The initial Nepokroeff et al. (2003) phylogeny was used as a test case for a new method for inferring geographic range evolution (Ree & Smith 2008), and then again to test yet another new method (Matzke 2014), but a better phylogeny would help to more accurately infer geographic range evolution. Hawaiian *Psychotria* exhibits variation in distribution within and across the Hawaiian islands, which prompts the following general questions. Why do some species occupy one or two islands, while some occupy many islands? And why are some species rare, some extremely rare, whereas

others are more common? Can species' climate niche or dispersal characteristics help explain these patterns?

For this thesis, I had six specific objectives:

1) Develop a robust molecular phylogenetic hypothesis for the evolutionary relationships of Hawaiian *Psychotria* species using multiple nuclear and chloroplast DNA markers and multiple, widely-sampled individuals per species.
2) Infer the climatic niches of the Hawaiian *Psychotria* species and calculate their climatic niche breadth using georeferenced collection records.
3) Test for the relative importance of three factors, species age, climatic niche breadth, and dispersal characteristics (seed size, body size), in explaining the variation in geographic distribution among species.
4) Build a more extensive molecular phylogenetic analysis of South Pacific *Psychotria* species by sequencing new species and combining my new data with previously published sequences.
5) Infer the ages and biogeographic history of the Hawaiian and South Pacific *Psychotria* species.
6) Infer climatic evolution of the South Pacific *Psychotria* species.

METHODS

Study Taxa and Ecological Context

The 11 Hawaiian *Psychotria* species are distributed across the six largest Hawaiian islands of Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii (Fosberg 1962, 1964; Sohmer 1977; Table 1). The Hawaiian species are mostly comprised of small trees and shrubs and are endemic to the Hawaiian Islands (Sohmer 1977). The number of independent introductions of Hawaiian *Psychotria* has been debated, with hypotheses stating either a single independent introduction (Fosberg 1962) or multiple (2 or 3) independent introductions (Sohmer 1978) resulting in the Hawaiian *Psychotria*. Taxonomically the genus, *Straussia*, as described by Asa Gray (1858) has long caused difficulties for accurate classification of Hawaiian plant species within *Psychotria*, due to high taxon complexity likely resulting from rapid diversification and hybridization among species of *Straussia* across the islands (Nepokroeff et al. 2003). In the early 1960s, F.R. Fosberg (1964) formally classified *Straussia* as a section within *Psychotria*, and described an additional section called *Pelagomapouria* (Sohmer 1977). The section *Straussia* is comprised of *P. fauriei, P. greenwelliae* (formerly named *P. psychotrioides*)*, P. hathewayi, P. hawaiiensis, P. kaduana, P. mariniana, P. mauiensis,* and *P. wawrae*. The section *Pelagomapouria* is comprised of *P. grandiflora, P. hexandra, and P hobdyi*. The classification of these divergent sections within Hawaiian *Psychotria* led S.H. Sohmer (1977) to hypothesize multiple independent colonization events rather than a single introduction onto the Hawaiian Islands. However, this theory remained inconclusive due to difficulties in classifying *Straussia* and *Pelagomapouria* species within the Hawaiian *Psychotria*. The *Straussia* species vary more intrinsically compared to the

Pelagomapouria species, which are found on older islands and tend to be the most distinct from one another (Sohmer 1978). Unlike the *Pelagomapouria* species, members of the *Struassia* section are more widely distributed across multiple islands. As they undergo adaptive radiation and/or hybridization after a dispersal event, they may tend to lose integral characteristics that allow for theses species to be easily distinguished from one another (Sohmer 1978). Recently Nepokroeff et al. (2003) inferred the first phylogeny of Hawaiian *Psychotria*, which revealed a significant finding. The Hawaiian species all formed a clade, indicating a single dispersal event. Furthermore, Nepokroeff et al. (2003) did not infer a time-calibrated tree, but they found a pattern of short branch lengths as is often found in phylogenies of other Hawaiian taxa (e.g., the Hawaiian silverswords; Baldwin 1991) that suggest a rapid radiation following a single introduction.

The Hawaiian Islands are the most isolated archipelago in the world (Fleischer et al. 1998) and home to over 1000 endemic plant species. The eight main islands (Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii) are composed in a linear array; from northwest to southeast arrangement. The Hawaiian Islands were established as the Pacific tectonic plate shifted and moved over volcanic regions (known as hot spots) forming a trail of active volcanoes. As islands shift away from the hot spot, they undergo subsidence and erosion creating atolls and seamounts (Fleischer et al. 1998). Potassium-argon (K-Ar) dating on lava surfaces of the Hawaiian Islands initially reported by I. McDougall (1964) suggests a methodology for island age estimation (Funkhouser et al. 1968). The oldest island of Kauai is dated at 5.1 million years ago (Ma), Oahu dated around 2.6-3.7 Ma, Molokai dated between 1.75-1.9 Ma, Maui is

1.32-0.75 Ma, and the youngest island of Hawaii is estimated to be at 0.43 Ma (Clague & Dalrymple 1987). Further K-Ar dating from Carson & Clague (1995) suggested the Maui, Lanai, Molokai, and Kahoolawe islands were connected around 0.3-0.4 Ma, an island known as Maui Nui. After formation of West Molokai, the island was connected to Oahu for a duration of 0.3 million years (Carson & Clague 1995). The Hawaiian islands are an exemplary model for island biogeography studies because age determination of individual islands via K-Ar dating can allow island age to be associated to biological events such as speciation (Dixon et al. 2011).

In the larger context of the South Pacific, island chains across the Pacific were formed from hot spots caused by the subduction of the Pacific Plate and now extinct Izanagi and Kula plates (Neall & Trewick 2008), generating numerous linear arrays of magma-filled volcanic arcs and subsequent submarine seamounts. Especially during Quaternary time, there were additional processes that influenced the formation of these islands such as fluctuating sea levels during periods of glaciations and interglaciation, which created the effect of linking islands and greatly influenced biodiversity across islands (Neall & Trewick 2008). Across Oceania, there are five subregions of islands. Continental Asia includes islands such as Japan, Philippines, Palau, Bonin Islands, and Taiwan. Japan consists mainly of four big islands, referred to as the 'Home Islands': Hokkaido, Honshu, Shikoku, and Kyushu. In addition there are over 6000 smaller islands within the archipelago of Japan which happens to be the largest archipelago in the Pacific, formed by the subduction of the Pacific plate beneath the Eurasian plate (Neall & Trewick 2008). Japan is mountainous and still holds volcanic activity. The Izu-Bonin-Islands extend off the coast of Japan, formed by subduction of the North New Guinea plate (now extinct) into the Eurasian plate

in between 50 and 40 Ma (Neall & Trewick 2008). Palau consists of 12 inhabited and over 700 small islands encased with rich and diverse landforms and climate. As a result, there is a large number of endemic species and the flora is richest in Palau compared to other regions of Micronesia (Canfield 1981). The subregion Melanesia, consists of the Solomon Islands, Papua New Guinea, Fiji, New Caledonia, and Vanuatu. The Solomon archipelago is comprised of seven major Solomon islands spanning the western Pacific Ocean along with islands of Papua New Guinea. Most regions of the Solomon Islands are of dense tropical rainforest with consistent annual temperature (28-30°C; Neall & Trewick 2008). Fiji consists of 332 islands, with the two largest being Vanua Levu and Viti Levu. Fiji has a very mountainous landscape where it was once covered in dense tropical rainforest (Neall & Trewick 2008). New Caledonia is comprised of the Grande Terre Island, Isle of Pines, and the Loyalty Islands. The mountains on Grande Terre form a divide on the island, humid east coast and dry west coast (Neall & Trewick 2008). Low levels of nitrogen, potassium, calcium, phosphorus in the soil on New Caledonia drive flora richness (Jaffre et al. 1987). The Polynesia subregion includes New Zealand, Samoa, Society Islands, and Austral Islands. Around 90 Ma a land mass known as Zealandia, began to separate from Gondwana and underwent sea-floor spreading and subsiding, eventually forming the region of New Zealand (Mortimer 2004). New Zealand today consists mainly of two large islands, North and South Island, and two small islands, Chatham and Stewart. The Society Islands are comprised of five groups, two of which are the main island of Tahiti and French Polynesia. This tropical archipelago was thought to have formed from a hotspot near Mehetia island, one of the Society Islands, east of Tahiti (Devey et al. 1990). Its mean annual rainfall range is 1700 mm (sea level) to 8000 mm (mountains), with an annual temperature of ~26°C (Neall & Trewick

2008). Continental Australia, the last subregion, consists of Australia, Tasmania, and a large number of smaller islands.

Remarkably, *Psychotria* species have managed to colonize all the subregions mentioned above, despite the large area encompassed by Oceania and the huge distances of unsuitable habitat (ocean) separating successful colonizations. There has been a massive diversification (> 100) of *Psychotria* species in New Caledonia (Barrabé, et al. 2014), and Fiji, Samoa, and the Mariana Islands all have sizable but poorly described species pools. In addition, the Philippines has over 100 described species (Sohmer & Davis 2007), including many endemic species, although due to catastrophic deforestation over that past few decades, many of these species are likely extinct. Finally, Papua New Guinea likely also harbors well over 100 species, many of which remain undescribed (S. Sohmer, *personal communication* with J. Paul).

MOLECULAR METHODS

Sampling of Taxa and DNA Extraction

For this study I obtained vouchered leaf tissue samples and some of the species included are represented by multiple individuals (refer to Table 2). I obtained silica-dried samples from six Hawaiian *Psychotria* species (two of which are *P. grandiflora* and *P. hobdyi*, federally listed rare and endangered species) and eight South Pacific *Psychotria* species from the collections of the National Tropical Botanical Garden (NTBG) in Kauai, Hawaii with the help of our collaborators, Dr. David Lorence and Dr. Kenneth Wood at NTBG. The few previously sequenced South Pacific species were inferred to be the putative closest relatives of the Hawaiian *Psychotria* by

Nepokroeff et al. (2003). I also obtained samples from 15 New Caledonian *Psychotria* species from the Missouri Botanical Garden in St. Louis, Missouri. In addition, our collaborator, Dr. Kenta Watanabe of the Okinawa National College of Technology in Japan, who is studying the breeding systems of Hawaiian *Psychotria*, shared silica-dried leaf tissue samples of his collections with us, which included samples from 10 Hawaiian and six Japanese *Psychotria* species, most represented by multiple individuals. DNA from leaf samples was extracted using a modified version of the Alexander et al. (2007) protocol for plant DNA extraction. All extracted DNA products were run on 1.5% agarose gel using GelRed and observed for band brightness under ultraviolet light to determine extraction quality.

DNA Marker Selection

The Hawaiian and South Pacific *Psychotria* samples I acquired were used to amplify and sequence a set of DNA markers (nuclear ribosomal and chloroplast) for phylogenetic inference. Nuclear markers included in this study were the internal- and external-transcribed spacer (ITS and ETS, respectively) regions of the nuclear ribosomal DNA genome. The ITS/ETS markers are generally easy to amplify via polymerase-chain reaction (PCR), widely used, and can be phylogenetically informative (Álvarez & Wendel 2003), particularly when used together (Logacheva et al 2010). However, these loci can be problematic in some taxa because they are multicopy loci (Baldwin et al. 1998), meaning that it can be potentially difficult to distinguish orthologs (homologous loci) from paralogs (gene duplications). In many taxa the multiple ITS copies appear to undergo concerted evolution via homologous recombination (Naidoo et al. 2013), whereby paralogs within a given species show higher sequence similarity to one another

than to members of their own gene family in other taxa. Hence, in taxa that have strong concerted evolution, the multicopy nature of these ribosomal markers does not impede their phylogenetic utility, and in fact ITS has been one of the most widely used and successfully employed nuclear markers for species-level plant phylogenies (Pozcai & Hyvönen 2009). Furthermore, since the nuclear genome is diploid (or of a greater ploidy), the effective population size of the nuclear genome is twice that (or more) of the haploid chloroplast genome. This is critical because it means that on average nuclear gene copies take twice as long to coalesce in the past compared to plastids genes; hence nuclear genes in recently diverged species may retain ancestral polymorphisms, leading to incomplete lineage sorting between loci, and the potential to infer false evolutionary relationships (Pillon et al. 2013).

The plastid regions of the chloroplast DNA genome known as chloroplast markers have played a central role in plant phylogenetics, especially for inferring generic and family-level relationships (Palmer 1985; Kårehed et al. 2008). For inferring low-level phylogenetic relationships, some chloroplast loci, particularly 'class II introns' (e.g., matK, rps16) have proven useful (Kelchner 2002). Chloroplast markers can often be amplified by near universal primers that are located in highly conserved exons (Kelchner 2002), and in most angiosperm lineages chloroplasts are maternally inherited via seeds, and reflect the history of seed dispersal and colonization within a lineage (Patwardhan et al. 2014). In addition, the chloroplast genome has other traits that are generally beneficial for phylogenetic inference - it is haploid and most loci are single copy (Kelchner 2002). A haploid genome means that on average chloroplast gene coalesce two times faster than nuclear genes, so chloroplast markers can show reciprocal monophyly between species much sooner in evolutionary time than nuclear genes (Pillon et al. 2013). However, the

plant chloroplast genome has a slower rate of evolution than the nuclear genome (Clegg et al. 1994), so chloroplast markers, when used individually or when only a few loci are combined, may lack sufficient variability to be useful for species-level phylogenetics (Pillon et al. 2013). However, recent research has identified additional chloroplast markers that appear to be highly variable across species and potentially useful for infrageneric studies (e.g., Dong et al. 2012). Combining nuclear ribosomal and chloroplast markers can be particularly beneficial for successful plant species discrimination (China Plant BOL Group et al. 2011).

In general, the ribosomal nuclear and chloroplast markers described above often used for barcoding are known to work well in *Psychotria* and other genera within *Rubiaceae*. Thus these markers were used in this study to infer phylogenetic relationships between the Hawaiian *Psychotria* species (Table 5).

PCR Amplification - Nuclear Ribosomal Genome

Two nuclear ribosomal regions, the internal- and external-transcribed spacers (ITS and ETS), were amplified with their respective forward and reverse primers. The PCR reactions were carried out in reaction volumes of 25.63µL: 18µL pure H_20, 2.5µL 10X Buffer, 2.5µL $MgCl_2$, 0.5µL BSA, 0.5µL DMSO, 0.5µL dNTPs, 0.25µL forward and 0.25µL reverse primers, 0.125µL Taq, and 0.5µL DNA template. For the ITS region, the reactions were run using the following thermocycler conditions: 2 min at 94°C, 40 cycles of 30 sec at 94°C, 1 min at 48°C, and 1 min at 72°C, with an elongation period of 7 min at 72°C and final storage at 12°C (Sedio et al. 2013). For the ETS region, the reactions were run using the following thermocycling

conditions: 3 min at 94°C, 35 cycles of 30 sec at 94°C, 1 min at 50°C, and 1.5 min at 72°C, with an elongation period of 7 min at 72°C and final storage at 10°C (Barrabé et al. 2012).

PCR Amplification - Chloroplast Genome

The plastid regions were amplified with their respective forward and reverse chloroplast primers. PCR reactions for the following primers (psbE-petL, trnK-rps16, and trnT-psbD) were carried out in reaction volumes of 25.63µL: 18µL pure H_20, 2.5µL 10X Buffer, 2.5µL $MgCl_2$, 0.5µL BSA, 0.5µL DMSO, 0.5µL dNTPs, 0.25µL forward and 0.25µL reverse primers, 0.125µL Taq, and 0.5µL DNA template. The PCR reactions were run using the following thermocycling conditions: 5 min at 94°C, 30 cycles of 1 min at 94°C, 30 sec at 54°C, and 45 sec at 72°C, with an elongation period of 5 min at 72°C and final storage at 12°C (Dong et al. 2013). PCR reactions for primers (matK-kim, psbA, rbcL, and rps16) were performed using the mentioned protocol in reaction volumes of 25.63µL. The samples were run using the following thermocycling conditions: 3 min at 94°C, 35 cycles of 1 min at 94°C, 1 min at 50°C, and 2 min at 72°C, with an elongation period of 7 min at 72°C and final storage at 10°C (Barrabé et al. 2012).

DNA Clean-Up and Sequencing

All amplified PCR products were run on 1.5% agarose gel using GelRed and observed for band brightness under ultraviolet light to determine the quality of amplification. Successful PCR products were cleaned up using the following exonuclease I-shrimp alkaline phosphatase protocol: PCR Clean-Up protocol in reaction volumes of 20µL: 12µL mixture of 10X Sap

Buffer, SAP, and EXO, and 7.5μL of PCR product. The cleaned-up PCR products were run on 1.5% agarose gel to check for the presence of successful bands. The purified PCR products were sent to two sequencing facilities to obtain reads of forward and reverse DNA sequences: the Cancer Research Center DNA Sequencing Facility in University of Chicago, Chicago, Illinois and the Molecular Cloning Laboratories (MCLAB) in South San Francisco, California.

DNA ALIGNMENTS

DNA alignments of the sequences were performed using MUSCLE algorithm (Edgar 2004) in the program Geneious v8.1.3 (Kearse et al. 2012). Alignment columns were manually edited to ensure the polymorphic sites were indeed polymorphic, ambiguous sites were coded as N, and all heterozygous sites from nuclear markers were assigned the proper ambiguity code (e.g., Y represent C or T). Final consensus sequences of the alignments were generated from the edits and used for phylogenetic inference (Table 6). I incorporated additional Hawaiian and South Pacific *Psychotria* species sequences retrieved from GenBank (Table 4) into phylogenetic analyses.

A Core Phylogeny of Hawaiian and South Pacific Psychotria

The first objective was to build on the previous phylogenetic work of Hawaiian *Psychotria*, performed by Nepokroeff et al. (2003), by utilizing more nuclear markers and introducing chloroplast markers for the first time. In addition, I incorporated more herbaria collections (i.e. multiple accessions per species and multiple accessions per island and/or regions of islands). I then inferred the phylogeny using Bayesian analyses with the 8-Loci alignment (Table 7), which

included both the two nuclear (ITS and ETS) and six chloroplast (psbA, psbE, rbcL, rps16, trnK, and trnT) genes.

An Extended Phylogeny of Hawaiian and South Pacific Psychotria

The second objective was to expand on our robust phylogeny by incorporating additional Genbank sequences of Hawaiian and South Pacific *Psychotria* from previous studies in order to strengthen the inferred relationships among the Hawaiian species and infer which South Pacific species is the closest relative to Hawaiian *Psychotria*. I inferred the phylogeny using Bayesian analyses with the 6-Loci alignment (Table 7), which included both the two nuclear (ITS and ETS) and four chloroplast (matK, psbA, rbcL, and rps16) genes.

A Combined ITS, ETS, and rps16 Phylogeny of Hawaiian and South Pacific Psychotria

The third objective was to build a supermatrix phylogeny of Hawaiian and South Pacific *Psychotria* by utilizing more taxa samples of *Psychotria* from Genbank in order to observe any evolutionary changes in the nuclear genome of Hawaiian and South Pacific *Psychotria* combined with the rps16 chloroplast genome. I inferred the phylogeny using Bayesian analyses using the 3-Loci alignment (Table 7), which included both the two nuclear (ITS and ETS) genomes and the rps16 chloroplast genome.

A Chloroplast Phylogeny of Hawaiian and South Pacific Psychotria

The fourth objective was to build a chloroplast phylogeny of Hawaiian and South Pacific *Psychotria* by utilizing only chloroplast markers in order to observe any evolutionary changes in

the chloroplast genome of Hawaiian and South Pacific *Psychotria*. I inferred the phylogeny using Bayesian analyses using the Chloroplast-Loci alignment (Table 7), which included 6 chloroplast (psbA, psbE, rbcL, rps16, trnK, trnT) genomes.

I chose to utilize these four main alignments to infer phylogenetic relationships among the Hawaiian and South Pacific *Psychotria* for a couple of reasons. The Rubiaceae, being one of the largest angiosperm families, is highly morphologically diverse, however at the same time is difficult to classify infra-familially because of a lack of unique morphological characters (Bremer et al. 1999). Thus, molecular phylogenetic analysis is required for this level of infrafamilial classification. A key concern is the lack of support for nodes in a phylogeny, but several methods have been proposed to obtain better support: adding more taxa and characters. The obstacle is understanding the effect of adding more taxa or more characters on the inferred relationships. How well supported are the nodes in phylogenetic trees produced with additional taxa or characters numbers? Will adding more taxa yield a stronger, more robust phylogeny, or will adding characters be a better approach? Several phylogenetic studies in the past have revealed two unique outcomes. One performed by Graybeal (1998), used more taxa and fewer characters to improve the support of nodes. The other study by Poe and Swofford (1999) showed that adding more characters greatly improved accuracy even for long branching trees, but adding taxa can reduce topological accuracy if slowly, evolving markers are used. In a more recent study on *Rubiaceae*, Bremer et al. (1999) revealed a positive correlation with adding more characters and the percentage of supported nodes within a given tree. On the contrary, adding more taxa resulted in negative correlation for supported nodes. Our goal in this study was to

improve upon the past phylogeny of the Hawaiian *Psychotria* species, which initially lacked many individuals and included relatively few characters. By incorporating more taxa and characters that we have sampled and from past studies into these four alignment scenarios, I hope to more clearly elucidate the relationships within the Hawaiian species and the relationship between the Hawaiian and South Pacific *Psychotria*.

The other impact on building phylogenies is the effect of missing data incorporated into phylogenetic analysis. Missing data can come from the lack of taxa or missing data cells such as loci markers for each taxa or missing character states within markers. Phylogenies with incomplete taxa have been hypothesized to suggest unresolved relationships among taxa because of the lack of characters to accurately place them on a phylogeny (Huelsenbeck 1991). Phylogenies with incomplete character states can also be an issue because lacking data cells has been proposed to increase ambiguity in having resolved character states at the nodes of a phylogeny (Wiens 2003). From studies on phylogenetic stimulation and analysis (Wiens 2006), missing character states were shown to have a greater impact on the phylogeny than having missing taxa. A phylogeny with incomplete taxa can lead to low resolution, but having a greater ratio of resolved character states can still correctly reconstruct the phylogeny. Our goal was not only to increase sampling of taxa, but also increase the amount of resolved character states (e.g., markers) to strengthen the species relationship of the Hawaiian species.

PHYLOGENETIC METHODS

Inferring Phylogenies and Divergence Times

Successful sequence alignments were used to reconstruct the phylogenetic relationships of *Psychotria* species. Phylogenies depict the evolutionary history shared among species. Phylogenetic inference is a tool used to determine evolutionary history through methods that would ultimately depict the best phylogenetic tree. In a given group of species, a higher number of study taxa constitutes a greater number of possible tree topologies (tree space - showing all possible combinations of relationships among taxa). Often times, searching tree space using algorithms (e.g. branch and bound, heuristic search) can reduce the number of possible trees (Felsenstein 2004) and make searching tree space more efficient. Various methods of phylogenetic inference include parsimony, maximum likelihood, and Bayesian inference. These methods vary in strengths and weaknesses. Parsimony is fast and quite accurate, but not statistical (Felsenstein 2004). This method is based on the assumption that the tree with the fewest number of evolutionary changes represents the evolutionary history for a given group of species. Unlike parsimony, maximum likelihood and Bayesian inference require using a model of evolution (Darriba et al. 2012). A model of evolution describes rates and probabilities of DNA substitutions and is assumed to be correct for a particular maximum likelihood and Bayesian analysis. Maximum likelihood depicts the tree with the highest likelihood (for a given model of evolution) as the best tree. This method is relatively slow, but highly accurate, assuming that the underlying model of molecular evolution is a good approximation of reality. Bayesian inference results in the best trees with the highest posterior probabilities (for a given model of evolution). Bayesian analysis is relatively slow, but this newer method also incorporates likelihood and prior

assumptions. These previous assumptions known as prior probabilities can be either informative or uninformative parameters. Bayesian inference uses markov-chain Monte Carlo (MCMC) to integrate priors and data to sample from the stable posterior distribution and infer the trees the highest posterior probabilities. The disadvantage of Bayesian inference is the unknown effect of prior probabilities and how to determine which type of priors are reasonable enough to use for inference (Felsenstein 2004).

In this study, I used Bayesian relaxed phylogenetic analyses (program BEAST v1.8.2; Drummond et al. 2012) to simultaneously infer phylogenetic relationships and divergence times among the Hawaiian taxa and other South Pacific *Psychotria* species. I also used maximum likelihood (program RaxML; Stamatakis 2014), and parsimony (program PAUP* v4b10; Swofford 2003) analyses to support the results of the BEAST analyses. The program JmodelTest2 (Darriba et al. 2012) was used to compare models of molecular evolution and the most appropriate model was chosen for a given data set for Bayesian and likelihood analyses. The incongruence length difference (IDL) test (Farris et al. 1995) as implemented in the program PAUP* v4b10 (Swofford 2003) tested for congruence between and among nuclear ribosomal and chloroplast markers. If incongruence was not detected, all markers were combined into a single analyses, and if incongruence was detected, phylogenetic analyses were run on the different loci separately. Clade credibility was measured using posterior probability for Bayesian analyses and bootstrapping for maximum likelihood and parsimony analyses. Finally, I inferred divergence times in BEAST using a secondary calibration point derived from the analyses of New Caledonia *Psychotria* species by Barrabé et al. (2014). Secondary calibration uses divergence time

estimates from other studies to place constraints on nodes. Rubiaceae has a poor fossil record, and a few different studies have all converged on the same approximate ages of the main *Psychotria* clades (Paul et al. 2009, Sedio et al. 2013, Barrabé et al. 2014, Bremer & Eriksson 2009). BEAST allows the constraints on nodes to be statistical distributions, rather than point estimates, which is a great advantage since fossil ages are usually only known with large degrees of error. Specifically, I constrained three nodes in my analyses using secondary calibration based on the ages found in Barrabé et al. (2014). I used the point estimates inferred in that study as the median age of the node, and constrained the range of ages to match the 95% highest posterior density (HPD) inferred for each node. The following constraints were applied to the same nodes in the trees inferred using all four of our alignments. The root node of the phylogeny (which is a basal split between the *Psychotrieae* clade and its sister group *Palicoureae*, some species of which still hold the name *Psychotria* but are in this separate lineage), was assigned a log-normal distribution with a median of 39.5 Ma and a range from 30.5 - 54 Ma. This corresponds to the stem node of the *Psychotrieae*. The stem node of the Pacific clade was assigned a normal distribution with a median of 22 Ma and a range from 15 - 30 Ma. Finally, the crown node of the Pacific clade was assigned a normal distribution with a median of 14.5 Ma and a range from 9.5 - 21 Ma. The results of these divergence time estimates provide species ages for my analyses explaining variation in abundance.

Inferring Historical Biogeography

In order to understand the historical biogeography of the Hawaiian and South Pacific *Psychtoria*, I also used BioGeoBEARS (Matzke 2013) in program R in combination with phylogenetic

analysis (BEAST chronogram) and coded geographic ranges to infer the ancestral states of *Psychotria*. Ancestral range reconstruction presents a unique situation when trying to infer ancestral states because the geographic range is a different sort of character than a morphological trait, since speciation can result in range splitting and descendants can 'inherit' part of the range, something that is not possible in morphological traits, for example (Ree and Smith 2008). The Hawaiian *Psychotria* have played a central role in the development of methods to infer ancestral geographic ranges. First, the Nepokroeff et al. (2003) study of Hawaiian *Psychotria* was also a methodological paper introducing a new maximum likelihood ancestral state reconstruction method, as most previous methods were based on parsimony. Next, Ree and Smith (2008) used the same Nepokroeff et al. 2003 phylogeny and range data to introduce a new likelihood method of ancestral state reconstruction specifically designed for geographic range evolution, called LaGrange. Most recently Matzke (2014) developed the R package BioGeoBears, which build on and extends the methods of LaGrange. BioGeoBears can run three different classes of models dispersal-extinction-cladogenesis (DEC), dispersal-vicariance (DIVALIKE), and a Bayesian method called BayArea (BAYAREALIKE). Each of the models also has a '+J' option which allows for 'found-event' speciation (Matzke 2014). I ran all biogeographic models in BioGeoBEARS to infer the historical biogeography of the South Pacific *Psychotria* as a clade, as well as specifically analysing the Hawaiian radiation.

Inferring Haplotype Networks

I also built a minimum spanning network (Bandelt et al. 1999) using the program PopART (http://popart.otago.ac.nz) to look for the patterns of relationship between haplotypes and infer

missing haplotypes with the statistical parsimony method (Templeton et al. 1992). These analyses provide information about the order of divergence of chloroplast haplotypes, which when coupled with geographic information can provide information about patterns of seed dispersal across the Hawaiian islands.

ECOLOGICAL NICHE MODELING

In order to build ecological niche models of the Hawaiian *Psychotria* species, I used the program MaxEnt (v3.1.2; Phillips et al. 2006). MaxEnt uses the method of maximum entropy to ascertain optimal species distribution modeling (Phillips et al. 2004) and typically has greater performance compared to other approaches for niche modeling (Elith et al. 2006), especially under constraints of small sample sizes or limited data from collection records (Hernández et al. 2006). For each of the Hawaiian species, latitude and longitude values were extracted from occurrence data in the GBIF database (http://www.gbif.org), the NTBG collection database, and additional values were provided by Dr. Kenta Watanabe (Table 8). Nineteen bioclimatic variables and altitude were extracted from the WorldClim database (http://www.worldclim.org/bioclim; Table 9), a widely used source of climatic data for ecological niche modeling. Bioclimatic variables were derived from raw monthly precipitation and temperature values to create more biologically meaningful parameters (e.g., Min Temperature of Coldest Month, Precipitation of Wettest Quarter, etc.; see Table 9). Since these variables can be highly correlated, I first ran a correlation matrix on 1000 random points drawn for the climate layers for our study region. I chose eight variables that showed little correlation for our MaxEnt runs (Table 9). I then used custom R scripts to extract the bioclimatic data for each species' collection points. During our summer 2016 field expedition

in Kauai, we were able to establish reasonably approximate latitudes-longitudes for some of the specimens found on Kauai that had detailed records of site descriptions, thus increasing our sample size for niche modeling. Ultimately, these location values and climate variables were input to MaxEnt to infer climatic niche models using pairwise overlap.

I also used all nineteen bioclimatic variables to assess the distribution of South Pacific and Hawaiian *Psychotria* species in climatic space using principal component analysis (PCA) in R. I extracted climate data for a subset of the South Pacific *Psychotria* species for which there were georeferenced collection records (36 species). To compare the species in the Hawaiian clade to other clades in the South Pacific species, I calculated a species mean for each climate variable. I visualized the distribution of individuals (Hawaiian taxa) or species means (South Pacific) in the first two orthogonal PC axes and recorded the loading of the bioclim variables (their importance for a principal component axis).

The results of these models were used to predict regions of suitability for each species (Paul et al. 2009) and niche breadth (Sheth & Angert 2014) in order to compare and contrast niche characteristics with range size between species. The program ENMTools (Warren et al. 2010) was used to infer climatic niche overlap (degree of shared niche space) between species and test for niche identity (tests whether two niches are identical) between populations of species found on different islands or different mountain chains on the same island. Niche breadth was quantified as the range of climatic values inferred via ENMs for each species.

DISPERSAL ABILITY

Plants can only disperse during their seed stage, hence the most important dispersal characteristics for plants are related to seed characteristics. Recent studies show a direct correlation between certain species life-history traits (e.g. plant height and fruit size) with seed dispersal distance (Muller-Landau et al. 2008). In one of these studies, plant height has actually been found to be a better predictor of seed dispersal distance than seed mass (Thomson et al. 2011), so we also included plant height as a factor in our tests. Why is this the case? In terms of biotic dispersal, all *Psychotria* species have bird-dispersed fruits (Nepokroeff et al. 1999), but the seeds differ in size. In bird dispersed fruits, the fruit and seed size a bird can ingest is limited by its gape size, with larger birds dispersing larger fruits and seeds (Wheelwright 1985). Therefore, highly mobile birds may find a greater attraction toward tall species with large sized fruits, in which they will carry for long distances (Thomson et al. 2011). On average, large birds have larger home ranges and average dispersal distances, hence large birds may be expected to disperse seeds longer average distance (Howe & Smallwood 1982). For this study in particular, chloroplasts are often maternally inherited via seeds. Hence, I also took the phylogenetic approach and used chloroplast data in one way to infer historical seed dispersal patterns across islands and the other to project the level of dispersal ability within Hawaiian *Psychotria*.

STATISTICAL TESTS

Ultimately, I combined the results I inferred via my molecular phylogeny and ecological niche modeling to test if species age, ecological niche breadth, or dispersal characteristics can explain the variation in geographic range size among the Hawaiian species. I used multiple regression to

test the relative importance of species age, ecological niche breadth, and dispersal characteristics (fruit size and plant height) in explaining the number of islands that *Psychotria* species occupy.

RESULTS

PHYLOGENETIC ANALYSES

A Core Phylogeny of Hawaiian Psychotria

There is stronger support for the nodes in the current phylogeny (Figure 2a-c) compared to the initial phylogeny of Nepokroeff et al. (2003). The Hawaiian *Psychotria* are supported as a monophyletic lineage that arose from a single colonization event about 8.73 Ma with a high posterior probability of 1 (Figure 2b). The two most basal lineages, *P. hexandra* and *P. hexandra var. oahuensis,* have the earliest divergence from the one individual, *P. mariniana* on Kauai. However, the chloroplast phylogeny (Figure 6b), places this individual in the *P. mariniana* clade with high support. The two rarest species, *P. grandiflora* and *P. hobdyi*, which are only found on the northwest corner of Kauai, diverged from one another about 3.51 Ma (Appx. A). Sequencing multiple individuals per species indicates the four most basal species are reciprocally monophyletic (e.g. *P. hexandra var. oahuensis, P. hexandra*, *P. hobdyi*, and *P. grandiflora*). The more intermediate lineages (e.g, *P. wawrae, P. mariniana, P. greenwelliae, P. hathewayi, and P. fauriei)* were relatively monophyletic with high support, with a few exceptions suggesting either misidentified collection or a case of hybridization (e.g. one individual of *P. mauiensis* found in *P. greenwelliae* clade). However, the younger species (*P. kaduana, P. mauiensis,* and *P. hawaiiensis)* appear to be polyphyletic. There is much lower support for these more recently derived lineages as a whole clade suggesting the possibility of rapid radiation over a short period of time resulting in lower clade credibility. The addition of more samples for each species incorporated with additional markers improved inferences of species relationships for the basal

and intermediate lineages. Species that are found on multiple islands and have multiple individuals within a given population tend to group together starting on Kauai all the way across the islands, showing older to younger island colonization. For example the *P. mariniana* clade, found on Kauai later diversified on to Oahu and Molokai. Additionally, there is strong monophyletic support for the multiple individuals of a given species from the same island grouping together across the whole Hawaiian clade. Overall, our core results largely support the results of Nepokroeff et al. 2003. The addition of chloroplast sequences strengthened the support for inferred relationships of basal Hawaiian species.

Divergence Times - for the Core Phylogeny of Hawaiian Psychotria

From analysis using BEAST, the median divergence time for the stem node of the Hawaiian clade is inferred to be about 8.73 Ma. (Table 10; node age range in Appx. A).

The crown median divergence time for species within the *P. hexandra* - *P. hexandra* var. *oahuensis* clade is 2.5 Ma, within the *P. grandiflora* - *P. hobdyi* clade is 3.51 Ma, within the *P. mariniana* - *P. wawrae* clade is 4.01 Ma, and within the *P. greenwelliae* - *P. mariniana* clade is 6.33 Ma.

An Extended Phylogeny of Hawaiian and South Pacific Psychotria

There is stronger support for many phylogenetic relationships among the Hawaiian species with other South Pacific species based on the inferred phylogeny (Figure 3a-c) from integrating sequence data from previous studies on *Psychotria*. The closest living relatives of the Hawaiian *Psychotria* appear to be a clade from the Philippines and Papua New Guinea (*P. cadegensis* and

P. sp respectively; Figure 3c), which is shown by the single divergence of the Hawaiian clade from the South Pacific around 9.3 Ma. The results of this phylogeny are largely congruent with the previous core phylogeny of the Hawaiian species. The most basal lineages were consistent in grouping together monophyletically with high posterior support values. Similar to the core phylogeny, the recently derived species in the *P. hawaiiensis* clade, sister to the *P. greenwelliae* clade have a low posterior support value and show relatively very short branching and polyphyletic species relationships within the clade. A majority of the taxa incorporated from Genbank grouped into the same major clades as did in the core phylogeny.

Divergence Times - for the Extended Phylogeny of Hawaiian and South Pacific Psychotria

From analysis using BEAST, the median divergence time for the stem node of the Hawaiian clade is inferred to be about 7.24 Ma. (Table 10; node age range in Fig. 5a-c).

The crown median divergence time for species within the *P. hexandra* - *P. hexandra var. oahuensis* clade is 2.51Ma, within the *P. grandiflora* - *P. hobdyi* clade is 3.45 Ma, within the *P. mariniana* - *P. wawrae* clade is 3.82 Ma, and within the *P. greenwelliae* - *P. mariniana* clade is 5.35 Ma.

A Combined ITS, ETS, and rps16 Phylogeny of Hawaiian and South Pacific Psychotria

There is strong support for the phylogenetic position of the Hawaiian species among other South Pacific *Psychotria* species (Figure 4a-c). However, there is one collection allegedly from Guam that groups with the Hawaiian *Psychotria*, but this sequence from Nepokroeff et al. (1999) lacks voucher information and is likely a misidentification (Figure 4b). Furthermore, one other

non-Hawaiian species is found to be nested within the Hawaiian taxa, *P. chrysantha*, which is from Papua New Guinea (PNG). I do not interpret this as a case of dispersal to Papua New Guinea, however, since this species is only represented in this tree by one marker, rps16, which is relatively invariable compared to ITS and ETS. Hence, it seems likely that this species is misplaced here due to a lack of data, although its position within the Hawaiian species is interesting given that some of the closest living relatives of the Hawaiian species are also from PNG. The positions of the Hawaiian basal clades were largely congruent with the positions in the two previous phylogenies. In this phylogeny, the closest relative was shown to be *Psychotria* species from Papua New Guinea as suggested also in the previous phylogeny as one of the closest relatives to the Hawaiian clade (Figure 4c). Overall, the addition of more taxa result in a phylogeny largely congruent with the first two phylogenies given the positions of the clades for the basal lineages Hawaiian species. However, the majority of the major clades in this tree have low support values due to using a fewer number of markers.

Divergence Times - for the Combined ITS, ETS, and rps16 Phylogeny of Hawaiian and South Pacific Psychotria

From analysis using BEAST, the median divergence time for the stem node of the Hawaiian clade is inferred to be about 8.23 Ma (Table 10; node age range in Appx. B).

The crown median divergence time for species within the *P. hexandra* - *P. hexandra var. oahuensis* clade is 3.03 Ma, within the *P. grandiflora* - *P. hobdyi* clade is 4.51 Ma, within the *P. mariniana* - *P. wawrae* clade is 4.59 Ma, and within the *P. greenwelliae* - *P. mariniana* clade is 4.05 Ma.

A Chloroplast Phylogeny of Hawaiian and South Pacific Psychotria

The inferred chloroplast phylogeny (Figure 6a-c) shows some incongruence with the three previous phylogenies. There are two major split in clades with *P. grandiflora* being basal in one clade and *P. hexandra* being basal in the other, shown by the two earliest divergence within the whole Hawaiian clade. Based on the chloroplast data, the most basal lineage of the Hawaiian clade is *P. grandiflora* or *P. hobdyi*, not *P. hexandra* (Figure 6b). However, the support is low for both of the two major Hawaiian clades, likely due to the lack of variation within the chloroplast genome. The median divergence time of the Hawaiian clade from other South Pacific species of 9.21 Ma is slightly higher estimated from the other three inferred phylogenies due to the new topology within the Hawaiian clade (Appx. C). The position of *P. hexandra* falling within the intermediate lineages suggests an earlier divergence time for the split between *P. mariniana* and *P. greenwelliae*.

Divergence Times - for the Chloroplast Phylogeny of Hawaiian and South Pacific Psychotria

From analysis using BEAST, the median divergence time for the stem node of the Hawaiian clade is inferred to be about 9.21 Ma (Table 10; node age range in Appx. C).

The crown median divergence time for species within the *P. hexandra* - *P. hexandra* var. *oahuensis* clade is 1.63 Ma, within the *P. grandiflora* - *P. hobdyi* clade is 3.83 Ma, within the *P. mariniana* - *P. wawrae* clade is 5.73 Ma, and within the *P. greenwelliae* - *P. mariniana* clade is 9.21 Ma.

Historical Biogeography of Hawaiian and *South Pacific Psychotria*

The best ancestral states reconstruction using the 6-loci data and inferred by BioGeoBEARs analysis is shown as the 'Dispersal-Vicariance + founder event speciation' (DIVALIKE+J) model (Figure 7a, Table 11a). This model suggests that South Pacific species from the subregion of Micronesia had the earliest single divergence from the subregion of continental Asia at ~16.5 Ma, and for majority was confined in Micronesia. Species from the Melanesia region had a later single split at ~14 Ma from continental Asia. The Melanesian species maintain a monophyletic clade within the Melanesia region suggesting very low dispersal onto other islands outside of this subregion. The species in the Polynesia region show later divergences from within Micronesia and Melanesia regions at similar time frames of ~5.5 Ma. The Hawaiian clade diverged from continental Asia and/or Melanesian species around ~9.5 Ma and were confined on the Hawaiian Islands.

Historical Biogeography of Hawaiian Psychotria

The best ancestral states model inferred by analysis using BioGeoBEARS is shown as 'Dispersal-Extinction-Cladogenesis + founder event speciation' (DEC+J) model (Figure 7b, Table 11b). The results show *P. hexandra* clade to be the most basal clade on Kauai and there was a subsequent colonization onto Oahu leading to the divergence of *P. hexandra* var. *oahuensis* from its sister species, *P. hexandra* at ~2.5 Ma. The sister species *P. hobdyi* and *P. grandiflora* diverged from each other on Kauai around 3.5 Ma. The sister clade to *P. hobdyi* and *P. grandiflora* diverged from each other at ~7 Ma with a subsequent divergence into two main clades around 5.5 Ma. Within one of these two clades, *P. mariniana* on Kauai diverged from *P.*

wawrae at ~4 Ma and underwent subsequent colonization onto the islands of Oahu, Molokai, and Hawaii at ~3 Ma. For the second clade, the younger species diverged from *P. greenwelliae* around 3.5 Ma onto Oahu, then followed by subsequent colonization from Oahu on to Molokai and Hawaii at ~2.5 Ma.

Haplotype Network of Hawaiian Psychotria

I built a minimum spanning haplotype network (Figure 8) which showed a greatly diversified topology of the Hawaiian species geographically found on the islands which is largely congruent to the historical biogeography of the Hawaiian species. The center core group consists of the most basal Hawaiian lineage (*P. hexandra)* found on Kauai. The *P. hexandra var. oahuensis* haplotypes are directly linked to core *P. hexandra,* which suggests divergence of *P. hexandra var. oahuensis* from *P. hexandra* when dispersed onto Oahu. Haplotypes for *P. grandiflora and P. hobdyi* show direct linkage to each other, however they differ from *P. hexandra* by a great number of mutations. At intermediate positions, *P. mariniana* shows divergence onto several different islands. First on Kauai, then onto Molokai and Oahu, shown by the direct linkage between these haplotypes of *P. mariniana*. The core group of younger Hawaiian lineages (e.g., *P. mauiensis* and *P. hawaiiensis)* consists of a great number of similar haplotypes, which is concordant with the younger species being recent divergences and lacking the genetic variation to be genetically distinct from each other.

ECOLOGICAL NICHE MODELING

The results of the models (Figures 9a-m) show that the climatic niches vary across the Hawaiian species. For example, *P. grandiflora* has a very narrow habitat suitability, which suggests a small potential range (Figure 9b). The intermediate aged lineages such as *P. mariniana* have an intermediate level of habitat suitability (Figure 9j). The younger species such as *P. mauiensis* have a very broad habitat suitability, which suggests a larger potential range (Figure 9k). So there is general trend of the earliest diverging (oldest) Hawaiian species having very restricted climatic niches and more recently derived (young) species generally have much broader climatic niches.

Principal component analysis of the 19 bioclimatic variables across the Hawaiian *Psychotria* species resulted in two principal component axes that explained 98.4% of the variance (PC1 = 93.2%; PC2 = 5.2%). The loadings of the bioclim variables on the PC axes shows the relative contribution to the variables to each axis (Table 13a). For PC1, Bio12 (annual precipitation) was by far the most important factor, followed by relatively equal contributions from Bio16 (precipitation of the driest quarter), Bio17 (precipitation of the wettest quarter), Bio18 (precipitation of the wettest quarter), and Bio19 (precipitation of the driest quarter). In contrast, for PC2, Bio4 (temperature seasonality) was by far the most important factor, followed by the same four secondary factors that loaded strongly on PC1 (Bio15 - Bio19). A plot of these first two PCs is depicted in Figure 10a.

To contrast the Hawaiian species with other South Pacific species for which georeferenced data

were available (Appx. D), I calculated species means for each climatic variable, and then used PCA as in the analysis above. The loadings of the bioclim variables on the PC axes shows the relative contribution to the variables to each axis (Table 13b).The first two PCs explained 93.3% of the variance (PC1 = 74.4%; PC2 = 18.9%). For PC1, Bio12 was again by far the most important factor, followed a strong contribution from bio4 (temperature seasonality), followed by modest contributions from Bio17, Bio18, and Bio19. Also like the Hawaiian analysis, PC2's strongest contributor was Bio4, followed by a strong contribution from Bio12, and modest contributions from Bio18 and Bio19. A plot of these first two PCs is depicted in Figure 10b.

STATISTICAL ANALYSES

Niche Breadth

From the ENMTools analysis, the results (Table 12) show that for the majority of Hawaiian species found only on one island on average had very small niche breadths. *P. grandiflora*, considered one of the older species only found on Kauai, had the smallest niche breadth value of 0.0087. On the contrary, *P. mauiensis*, one of the younger lineages found on multiple islands, had the largest niche breadth of 0.6643. In general, I can see a trend of younger species having larger niche breadths compared to the older species. I also combined niche analysis of the recent lineages (e.g., *P. kaduana, P. fauriei, P. hathewayi, P. mauiensis,* and *P. hawaiiensis*) as one whole *P. kaduana* clade to infer the overall niche breadth, since these species shared a polyphyletic relationship. Thus, the result of the niche breadth for the combined *P. kaduana* clade is 0.6493, the second largest niche breadth after *P. mauiensis*.

Multiple regression

To assess what factors best explained variation in number of islands occupied, I conducted a multiple regression with 'number of islands' as the response variable and two metrics of species age, stem age (split from most recent common ancestor, Table 10), and crown age (earliest divergence within a lineage, Table 10), the two metrics of niche breadth, and two morphological characters related to dispersal, fruit size and plant height (Appx. E). I found a significant relationship overall (P = 0.04), with plant height being the only significant individual factor (Table 14).

DISCUSSION

Inferred Phylogenetic Relationships of Hawaiian Psychotria

In this study, I conducted phylogenetic analysis on species of Hawaiian *Psychotria* using additional taxa and markers that prior studies lacked. The inferred phylogenies in my study (Figures 2, 3, 4) that incorporated the combination of both nuclear and chloroplast markers resulted in very similar topologies, with a combined stronger support for inferred relationships in the Hawaiian clade compared to Nepokroeff et al.'s study (2003). In contrast to their previous study, the combination of more taxa and markers provided greater resolution for the relationships within the monophyletic clades for the older species. Similarly, *P. hexandra* is inferred to be the most basal and is sister to the rest of the Hawaiian species with 100% support. However, I saw relatively recent divergences within individuals of these species having low support due to little genetic divergence over a short period of evolutionary time (Figure 5a). Nepokroeff et al. (2003) mentioned that the combination of only using nuclear ITS and ETS markers inferred weakly supported paraphyletic relationships amongst *P. kaduana, P. fauriei, P. hathewayi, P. mauiensis,* and *P. hawaiiensis*. Similar to her results, I also saw low support for a clearly resolved relationship between these recently derived lineages, even after adding numerous individuals and additional loci. However, there is very high posterior support for the section of *Straussia* deriving from the *Pelagomapouria* section at ~6.55 Ma (according to the results of Figure 3a). This result supports Fosberg's (1964) hypothesis that members in the *Pelagomapouria* section gave rise to members of the *Straussia* section. The three members of the *Pelagomapouria*

section, *P. hexandra, P. grandiflora,* and *P. hobdyi,* are consistently inferred as the most basal lineages as stated by Sohmer (1978) and are phylogenetically distinct from members of the *Straussia* section.

Novel findings in this study include the one individual of *P. mariniana* as one of the basal lineages. This individual is inferred to be close relatives to the *P. hexandra* clade, possibly due to hybridization (Sohmer 1978) or the possibility of polyploidy within the nuclear genome that can affect phylogeny reconstruction (Nepokroeff et al. 2003). Polymorphic characters have also been hypothesized to affect phylogenetic inference (Sang et al. 1995). During the study, I came across multiple polymorphic characters in the DNA sequences of both the nuclear and chloroplast genomes used to infer the phylogenies. The nuclear genome is known to be variable and this grouping suggests this variability is driving this individual closer genetically to *P. hexandra*, even though it was classified morphologically as *P. mariniana.* Upon closer look at the chloroplast phylogeny, this individual groups together with other individuals of *P. mariniana,* suggesting this individual may have a *P. mariniana* chloroplast genome and a nuclear genome dominated by *P. hexandra*. This suggests that P. hexandra pollen may have pollinated a *P. mariniana* flower, creating a hybrid. . The other finding I have come across is the polyphyletic relationships among the younger lineages (e.g., *P. kaduana, P. fauriei, P. hathewayi, P. mauiensis,* and *P. hawaiiensis*). Nepokroeff's phylogeny shows a paraphyletic relationship among those species, but in our case, they seem to be grouping polyphyletically by geography. This suggests little genetic variation across morphologically divergent species, which can occur in very closely related species (Jang et al. 2009). This result is concordant with what Sohmer

(1978) initially proposed with sister species in section *Straussia* undergoing inter-island dispersal leading to adaptation from similar gene pools and similar habitats.

The haplotype network (Figure 7) inferred with chloroplast markers was largely congruent with the inferred relationships from the phylogenies. The direct linkage of multiple haplotypes to the core *P. hexandra* haplotypes suggests that the chloroplast data highly correlates with geographical distributions. This pattern is indicative of the Hawaiian species being each other's closest relatives given some occupy neighboring islands and some within the same islands. The linkage between several *P. mariniana* haplotypes from different islands shows that *P. mariniana* has dispersed onto multiple islands (e.g., Kauai, Molokai, and Oahu). The chloroplast genome also evolves at a much slower rate than the nuclear genome, hence there is less genetic variation within these closely related species. It is evident from the large haplotype group linking off from the core, which consists of the majority younger derived lineages whose little genetic variation due to recent divergence, share the very same chloroplast haplotype. This further suggests that morphologically divergent species on different islands are still very genetically similar. This result coincides with the younger species grouping together polyphyletically with low resolution, proving difficult to distinguish between each other.

After using chloroplast markers and additional taxa, I discovered strong support for the relationships among basal lineages within the Hawaiian species. However, among the recently derived lineages, there was much lower support suggesting the possibility of rapid radiation over a short period of time. This is surprising considering chloroplast typically evolve more slowly.

These results indicate the need for more markers to resolve these phylogenetics relationships within the clades; as well as test various additional nuclear (including possibly low-copy markers) and chloroplast markers that will aid in providing stronger support for the phylogenetic relationships among these closely related taxa.

Biogeographical History of Hawaiian Psychotria

The results of the ancestral states inferred from BioGeoBEARS is largely congruent with the inferred relationships and the geography of these species across the Hawaiian islands. In the comparison between Hawaiian and South Pacific species (Figure 8a), the Melanesian species maintain a monophyletic clade within the Melanesia region after early divergence from continental Asia, suggesting very low dispersal onto other islands outside of this subregion. An interesting finding is that major clades of species confined to one geographic location diverged at the same time as did other major clades from a different region. Even though there is great structure within each subregion of species, there are many parallel divergences of species across the subregions. For example, four divergences occurred relatively in the same time frame at ~9.5 Ma, within the clade of Melanesia species, and between species in the Melanesia region and the Hawaiian islands. This suggests other possible factors (e.g., common selective pressures due to changing climate regimes) may have caused these species to undergo relatively similar evolutionary changes during similar periods of time in different geographic regions (Tennessen & Akey 2011). In the comparison between only Hawaiian species (Figure 7b), the younger species are more widespread, found on multiple islands. The subsequent colonization of *P. mariniana* from Kauai onto islands of Oahu, Molokai, and Hawaii suggests that *P. mariniana* is

highly successful at dispersal across the islands. Similar for the majority of the younger species sister to the *P. greenwelliae* clade, they seem to have higher dispersal rates and potentially undergo frequent hybridization.

Ecological Niche Modeling of Hawaiian Psychotria

From the results of the models (Figures 9a-m), the earliest diverging (oldest) Hawaiian species have very restricted climatic niches, may which explain their narrow geographic distributions (being only on Kauai). These older species seem to only exist within a limited set of conditions that will allow them to persist without having to expand their habitat or acquire additional resources to survive. On the contrary, the more recently derived (young) species generally have broader climatic niches which is mostly true given they are more widespread and are found on multiple islands. Thus, the younger species should have larger geographic ranges and the potential for broader distributions, due to having broader climatic niches (Slayter et al. 2013). However, this is still questionable due to the fact that the younger species are more likely to be polyphyletic. So when multiple lineages are grouped into a single species for niche analysis, in the case of most of the recently diverged lineages, this could result in overestimation of the niche and niche breadth, and ultimately overestimation in geographic ranges size. Past studies have shown complication in conservation assessments from overestimating niche breadths and geographic ranges (Jetz et al. 2008). This leads to future questions of whether these species have actually fill their potential ranges, and if not, do they have the potential for even broader distributions?

Niche breadth

From the results, there is a general pattern of younger species having larger niche breadths compared to the older species. *P. grandiflora*, one of the older species only found on the most northwest end of Kauai has a very small habitat range, thus had the smallest niche breadth value of 0.0087. It is indicative by that *P. grandiflora* has a very narrow geographic distribution and has a stricter range of niche characteristics. On the other hand, *P. mauiensis*, one of the younger lineages, had the largest niche breadth of 0.6643. *P. mauiensis* is known to be found on islands of Molokai, Lanai, and Maui. These three islands as stated by Sohmer (1978), acted as an "evolutionary filter." During the periods of adaptive radiation and hybridization after dispersal of *P. mauiensis* across these islands, sister species such as *P. mariniana, P. kaduana, and P. hathewayi,* all shared similar genetic elements of *P. mauiensis*. Thus, the inferred niche breadth is very broad. In general, I also combined niche analysis of the recent lineages (e.g., *P. kaduana, P. fauriei, P. hathewayi, P. mauiensis,* and *P. hawaiiensis*) as one whole clade to infer the overall niche breadth, since these species shared a polyphyletic relationship. Because of the similarly shared genetic variation across the younger lineages, classifying the niches of these species as whole can be an effective approach to seeing how their individual niches compare. Overall, the individual niche breadth shows levels of intermediate to broader niches for the younger species, but as a combined clade, it has the second largest niche breadth value, indicating that if these species are indeed polyphyletic, their overall clade-level niche is very broad.

Bioclimatic variables

The results of the PC analyses of the Hawaii and South Pacific species provide valuable insight into the potential drivers of species distributions. Looking at the Hawaiian species (Figure 10a-b) both *P. hobdyi* and *P. grandiflora* have very narrow distributions, yet these sister species appear to have diverged along two different axes. *P. hobdyi* varies little on PC1 (annual precipitation), but shows considerable variation in temperature seasonality, while *P. grandiflora* shows the exact opposite pattern. Unsurprisingly, widespread species like *P. marinina* and *P. hawaiiensis* have broad climate distributions, yet are conspicuously absent from some parts of climate species. Other species individuals, such as *P. wawrae*, tightly clustered in one part of climate space.

Looking across the South Pacific species, the main axes of differentiation (PC1) is again associated with annual precipitation, with a strong secondary influence of temperature seasonality. There is some degree of conservatism seen in the clades, within clades members (colors) groups loosely. However, there are many areas of climatic overlap, indicating these distinct clades that are largely occupying different parts of Oceania nonetheless occupy similar climatic space. This suggests, along with the results of BioGeoBears, that *Psychotria* species likely could find suitable habitat in regions in which in a given species' clade is not found, if they were able to disperse there.

Dispersal Characteristics

From the results of the multiple regression test, plant height showed a significant relationship ($P = 0.04$) with the number of islands occupied compared to fruit size (Table 14). This suggests plant height plays a more significant factor in dispersal ability than fruit size for the Hawaiian *Psychotria* species. For example, *P. mariniana*, one of the tallest Hawaiian species recorded at ~25m (Appx. E), is found to occupy across multiple Hawaiian islands (Figure 1), which suggests a high level of dispersal ability across these islands. On the contrary, *P. grandiflora*, one of the shorter species (~5m, Appx. E) is found only on Kauai, which suggests a lower level of seed dispersal ability. From the *P. mariniana* individuals we used to infer the chloroplast loci phylogeny, the seed dispersal history is indicative of *P. mariniana* dispersing across at least the islands of Kauai, Oahu, and Molokai (Figure 6b). Furthermore, past studies suggest taller species typically have greater lifespans than shorter species (Moles & Leishman 2008). Thus, species with longer lifespans generally require less investment in dispersal capacity (Thomson et al. 2011), which may ultimately reflect a plant's life history strategy for spatial rather than temporal dispersal, like in the case for *P. mariniana* occupying multiple islands at once.

Conclusion - Driver of geographic range variation

After taking the three main factors (inferred species age, estimated niche breadth, and dispersal characteristics) into account for the multiple regression test, the significant factor in driving island occupancy of Hawaiian *Psychotria* is found to be plant height, which we use as a proxy for dispersal ability. Even though species age and climate niche characteristics vary considerably

among species that are found across different islands, our results indicate dispersal ability, as described by plant height, is the most significant and reliable predictor of range variation relative to the other two factors in this study of Hawaiian *Psychotria*. As noted, dispersal is a key life history stage in plants. Distances in seed dispersal can greatly affect other important life stages such as migration, germination, persistence, and ultimately extinction (Howe & Smallwood 1982). Therefore, dispersal ability within a given plant species is a factor in which should be highly considered and further explored when looking at species abundance and distribution. Future tests on additional morphological traits (e.g. seed mass and seed size) may shed more light on the correlation between seed characteristics and dispersal ability relative to plant height and fruit size.

Limitations to this study

Several limitations in this study include developing or investigating more informative markers; especially for low-copy nuclear genes. Low-copy markers are not universal and typically require developing a new set of markers specifically for *Psychotria*. I am currently looking into other research that have incorporated low-copy genes (Sang 2002; Turner et al. 2013) into their phylogenetic analysis of taxa within Rubiaceae, which sets the basis on how to go about creating these markers. I did explore using a few low-copy nuclear markers, but failed to get them to sequence reliably. Another limitation is the lack of available georeferenced collection records required for analyses of ecological niche modeling. While there are many collection records for most of the Hawaiian species, many of these collections do not have latitude and longitude data. However, a large portion of these collections do include detailed location information, so I will

put considerable effort into establishing approximate latitude and longitude coordinates for these records to further improve the georeferenced data for these species.

Broader Impacts of this study

The study of Hawaiian *Psychotria* can be informative to the broader scientific community in several ways. A robust phylogeny of Hawaiian *Psychotria* will allow future researchers to answer other evolutionary and ecological questions about this model system. In addition, expanding the georeferenced collection records should be a benefit to the scientific community and conservationists by having more accurate geographic distribution records. On a global scale, phylogenetic study has been suggested to help with conservation implications. The conflict with conservation revolves around how to best allocate resources and how to prioritize conservation needs. Biologists and conservationists can integrate information on the evolutionary relationships between species to strategically allocate conservation efforts in maintaining ecosystem stability and species biodiversity (Rolland et al. 2012). Recently, conservation planners considered one method of allocating conservation resources that is based on phylogenetic distinctness. Conservationists refer to phylogenies to determine which clades of species would require more resources based on having the fewest number of taxa (Winter et al. 2013). Hence, understanding the evolutionary relationships among species can help conservationists develop ways to prioritize conservation efforts. My research has laid the groundwork for future researchers interested in explaining the distribution of species. I anticipate that my research will be an important piece of the puzzle regarding the distribution of Hawaiian taxa specifically, but also provide general insight for the study of species distributions.

TABLES

Table 1. Characteristics and locations of Hawaiian *Psychotria* species. An X means the taxa has been recorded on a given island. If a specific location is given, that means that is the only known location for a taxa on a given island.

Species	variety	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii	Conservation Status	US Status
P. fauriei			Ko'olau Mountains, O'ahu					Secure	none
P. grandiflora		(Koke`e; Alaka`i Swamp)						Endangered	Endangered
P. greenwelliae		(Koke`e)						Apparently secure	none
P. hathewayi	*brevipetiolata*		Wai'anae Mountains, O'ahu					Apparently secure	none
P. hathewayi	*hathewayi*		Wai'anae Mountains, O'ahu					Apparently secure	none
P. hawaiiensis	*hawaiiensis*			X		X	X	Apparently secure	none
P. hawaiiensis	*hillebrandii*			X		X	X	Apparently secure	none
P. hawaiiensis	*scoriacea*					X	X	Apparently secure	none
P. hexandra	*hexandra*	X						Apparently secure	none
P. hexandra	*oahuensis*		Ko'olau Mountains, O'ahu					Rare	Endangered
P. hobdyi		(Miloli`i-Kopiwai)						Endangered	Endangered
P. kaduana		X	X	X	X	X		Apparently secure	none
P. mariniana		X	X	X	X	X		Apparently secure	none
P. mauiensis		X		X	X	X	X	Apparently secure	none
P. wawrae		East Kauai						Rare	none

Table 2. Taxon samples of Hawaiian and South Pacific *Psychotria* species used for study, showing original voucher identification, the location the sample was originally collected.

Taxon	variety	Voucher ID	Location
Hawaiian *Psychotria*			
P. fauriei		K.M. Watanabe 4112	Kuliouou, Oahu
P. fauriei		K.M. Watanabe 4113	Kuliouou, Oahu
P. fauriei		K.M. Watanabe 4145A	Hawaii Loa, Oahu
P. fauriei		K.M. Watanabe 4145B	Hawaii Loa, Oahu
P. fauriei		K.M. Watanabe 4145C	Hawaii Loa, Oahu
P. grandiflora		D. Lorence 10461	Kokee, Kauai
P. grandiflora		K.M. Watanabe 5000	Kokee, Kauai
P. grandiflora		K.M. Watanabe 5001	Kokee, Kauai
P. grandiflora		K.M. Watanabe 5002	Kokee, Kauai
P. grandiflora		K.M. Watanabe 5003	Kokee, Kauai
P. grandiflora		K.M. Watanabe 5004	Kokee, Kauai
P. grandiflora		K.M. Watanabe 5005	Kokee, Kauai
P. greenwelliae		D. Lorence 10464	Kokee, Kauai
P. greenwelliae		K. Wood 15357	Koaie, Kauai
P. hathewayi		K.M. Watanabe 4264	Pahole, Oahu
P. hathewayi		K.M. Watanabe 4265	Pahole, Oahu
P. hawaiiensis		K.M. Watanabe 4250	Hawaiian Volcanoes, Hawaii
P. hawaiiensis		K.M. Watanabe 4251	Hawaiian Volcanoes, Hawaii
P. hawaiiensis		K.M. Watanabe 4252	Hawaiian Volcanoes, Hawaii
P. hawaiiensis		K.M. Watanabe 4276B	Hawaiian Volcanoes, Hawaii
P. hawaiiensis		K.M. Watanabe 4276C	Hawaiian Volcanoes, Hawaii
P. hawaiiensis		K.M. Watanabe 4276D	Hawaiian Volcanoes, Hawaii
P. hexandra	*hexandra*	D. Lorence 10465	Kokee, Kauai
P. hexandra	*hexandra*	D. Lorence 10466	Kokee, Kauai
P. hexandra	*hexandra*	K. Wood 15596	Iole, Kauai
P. hexandra	*oahuensis*	K.M. Watanabe 5300	Pahole Nursery, Oahu
P. hexandra	*oahuensis*	K.M. Watanabe 5301	Pahole Nursery, Oahu
P. hexandra	*oahuensis*	K.M. Watanabe 5302	Opaeula, Oahu
P. hobdyi		K.M. Watanabe 5104	Paaiki, Kauai
P. hobdyi		K.M. Watanabe 5153	Paaiki, Kauai
P. hobdyi		K.M. Watanabe 5192	Upper Mohanaloa, Kauai

P. hobdyi	K.M. Watanabe 5201	Mohanaloa, Kauai
P. hobdyi	K.M. Watanabe 5202	Mohanaloa, Kauai
P. hobdyi	K. Wood 15956	Kawaiula, Kauai
P. kaduana	K.M. Watanabe 4120	Kuliouou, Oahu
P. kaduana	K.M. Watanabe 4121	Kuliouou, Oahu
P. kaduana	K.M. Watanabe 4127	Tantalus, Oahu
P. kaduana	K.M. Watanabe 4130	Manoa Cliff, Oahu
P. kaduana	K.M. Watanabe 4249	Kaluaa, Oahu
P. mariniana	D. Lorence 10462	Kokee, Kauai
P. mariniana	D. Lorence 10463	Kokee, Kauai
P. mariniana	K.M. Watanabe 4122	Kuliouou, Oahu
P. mariniana	K.M. Watanabe 4169	Kamakou, Molokai
P. mariniana	K.M. Watanabe 4170	Kamakou, Molokai
P. mariniana	K.M. Watanabe 4261	Pahole, Oahu
P. mariniana	K.M. Watanabe 4262	Pahole, Oahu
P. mariniana	K.M. Watanabe 4263	Pahole, Oahu
P. mariniana	K. Wood 15591	Kalalau, Kauai
P. mauiensis	K.M. Watanabe 4171	Kamakou, Molokai
P. mauiensis	K.M. Watanabe 4176	Kamakou, Molokai
P. mauiensis	K.M. Watanabe 4177	Kamakou, Molokai
P. mauiensis	K.M. Watanabe 4178	Kamakou, Molokai
P. mauiensis	K.M. Watanabe 4179	Kamakou, Molokai
P. mauiensis	K.M. Watanabe 4184	Kamakou, Molokai
P. mauiensis	K. Wood 15547	Iliiliula, Kauai
P. wawrae	K.M. Watanabe 4037	Mt. Makaleha, Kauai
P. wawrae	K.M. Watanabe 4040	Mt. Makaleha, Kauai
P. wawrae	K.M. Watanabe 4041	Mt. Makaleha, Kauai
P. wawrae	K.M. Watanabe 4267	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4268	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4269	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4271	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4272	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4272B	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4272C	Mt. Anahola, Kauai
P. wawrae	K.M. Watanabe 4272D	Mt. Anahola, Kauai

P. wawrae		K.M. Watanabe 4272E	Mt. Anahola, Kauai
South Pacific *Psychotria*			
P. ammericola		G. McPherson 18065	New Caledonia
P. boninensis		K.M. Watanabe 0602	Chichijima, Bonin Islands
P. boninensis		K.M. Watanabe 0604	Chichijima, Bonin Islands
P. boninensis		K.M. Watanabe 0635	Chichijima, Bonin Islands
P. cephalophora		K.M. Watanabe 34011	Lanyu, Taiwan
P. cephalophora		K.M. Watanabe 34012	Lanyu, Taiwan
P. cephalophora		K.M. Watanabe 34013	Lanyu, Taiwan
P. comptonii		J. Munzinger 735	New Caledonia
P. faguetii		G. McPherson 18637	New Caledonia
P. fuscopilosa		P. Lowry 5631	New Caledonia
P. gabriellae		G. McPherson 18256	New Caledonia
P. garberiana		D. Lorence 8522	American Samoa, Tau
P. homalosperma		K.M. Watanabe 0142	Chichijima, Bonin Islands
P. homalosperma		K.M. Watanabe 0312	Anijima, Bonin Islands
P. homalosperma		K.M. Watanabe 0434	Hahajima, Bonin Islands
P. hombroniana		D. Lorence 9692	Palau (Belau)
P. hombroniana		D. Lorence 96156	Pohnpei, F.S.M.
P. hombroniana		S. Perlman 21427	Pohnpei, F.S.M.
P. hombroniana		S. Perlman 21482	Pohnpei, F.S.M.
P. hombroniana		K. Wood 13618	Kosrae, F.S.M.
P. kosraensis		K. Wood 14778	Kosrae, F.S.M.
P. lasianthoides		S. Perlman 21426	Pohnpei, F.S.M.
P. lepthothyrsa	*longicarpa*	S. Perlman 21184	Palau (Belau)
P. lyciiflora		G. McPherson 18203	New Caledonia
P. manillensis		K.M. Watanabe 2527A	Iriomote, Ryukyu Islands
P. manillensis		K.M. Watanabe 2701A	Okinawa, Ryukyu Islands
P. manillensis		K.M. Watanabe 34021	Lanyu, Taiwan
P. merrillii		D. Lorence 9611	Pohnpei, F.S.M.
P. merrillii		S. Perlman 21438	Pohnpei, F.S.M.
P. merrillii		S. Perlman 21444	Pohnpei, F.S.M.
P. mons-mi		P. Lowry 6811	New Caledonia
P. pancheri		G. McPherson 18550	New Caledonia
P. poissoniana		G. McPherson 18216	New Caledonia
P. pseudocollina		G. McPherson 18523	New Caledonia

P. pseudocollina		G. McPherson 18548	New Caledonia
*P. psychotrioides**		D. Lorence 7678	cult. at NTBG (origin: Sri Lanka)
P. pulchrebracteata		P. Lowry 6908	New Caledonia
*P. punctata**	*punctata*	D. Lorence 9196	cult. at NTBG (origin: Africa)
P. rhombocarpa		D. Lorence 10017	Kosrae, F.S.M.
P. rubra		K.M. Watanabe 2520A	Kakeroma, Ryukyu Islands
P. rubra		K.M. Watanabe 29502	Okinawa, Ryukyu Islands
P. rubra		K.M. Watanabe 3406	Lanyu, Taiwan
P. schlechteriana		G. McPherson 18206	New Caledonia
P. serpens		K.M. Watanabe 2511A	Amami, Ryukyu Islands
P. serpens		K.M. Watanabe 25322	Iriomote, Ryukyu Islands
P. serpens		K.M. Watanabe 29051	Kyushu, Japanese Islands
P. subpallens		G. McPherson 18103	New Caledonia
P. toninensis		G. McPherson 18512	New Caledonia
P. trisulcata		G. McPherson 18519	New Caledonia

* *Psychotria psychotrioides* is a species endemic to Sri Lanka, but leaf material was harvested from a plant growing at the NTBG in Kauai.

**Psychotria punctata var punctata* is a species endemic to continental Africa, but leaf material was harvested from a plant growing at the NTBG in Kauai.

Table 3. Hawaiian *Psychotria* and South Pacific *Psychotria* species from GenBank used for study, listing the GenBank accession number, the location of the voucher collection, and the reference in which the sequence was originally published.

Taxon	Location	Reference	*ITS*	*ETS*	*psbA*	*rbcL*	*rps16*
Amaracarpus grandifolius	Papua New Guinea	Andersson 2002					AF410678
Amaracarpus kochii	Papua New Guinea	Andersson 2002					AF410679
Amaracarpus muscifer	Fiji	Barrabé et al. 2014	KF675907	KF675790	KF676261		KF676083
Amaracarpus nematopodus	Australia	Barrabé et al. 2012	JX155060	KF675791	JX155192		JX155152
Amaracarpus nematopodus	Australia	Barrabé et al. 2012	JX155074				JX155166
Amaracarpus novoguineensis	Papua New Guinea	Razafimandimbison et al. 2014	KJ804785				
Amaracarpus pubescens var. sechellarum	Seychelles	Razafimandimbison et al. 2014	KJ804786	KJ804595		KJ805582	KJ805187
Amaracarpus sp.	Papua New Guinea	Razafimandimbison et al. 2014	KJ804787	KJ804596		KJ805583	KJ805188
Amaracarpus sp.	Papua New Guinea	Razafimandimbison et al. 2014	KJ804788	KJ804597		KJ805584	KJ805189
Anthorrhiza caerulea	Papua New Guinea	Chomicki and Renner 2016	KU586349	KU586368			
Anthorrhiza clemensii	Malesia	Nepokroeff et al. 1999	AF034915				
Anthorrhiza echinella	Papua New Guinea	Chomicki and Renner 2016	KU586350	KU586369			
Calycosia lageniformis	Fiji	Andersson 2002					AF410680
Calycosia aff. lageniformis	Fiji	Razafimandimbison et al. 2014	KJ804793	KJ804601		KJ805589	KJ805194
Calycosia cf. petiolata	Fiji	Barrabé et al. 2014	KF675908	KF675792	KF676262		KF676084
Calycosia macrocyatha	Fiji	Razafimandimbison et al. 2014					AF410681
Calycosia magnifica	Fiji	Razafimandimbison et al. 2014	KJ804794	KJ804602			
Dolianthus vaccinioides	Papua New Guinea	Andersson 2002 Razafimandimbison et al. 2014					AF410685
Hedstromia latifolia	Fiji	Barrabé et al. 2014	KF675911	KF675795	KF676265		KF676087
Hydnophytum cf. longistylum	Vanuatu	Barrabé et al. 2012	JX155078	KF675797	JX155209		JX155170
Hydnophytum formicarum	Unknown	Andersson 2002					AF001339
Hydnophytum formicarum	Malesia	Nepokroeff et al. 1999	AF034912				
Hydnophytum formicarum	Malaysia	Chomicki and Renner 2016	KU586346	KU586365			
Hydnophytum grandiflorum	Fiji	Razafimandimbison et al. 2014	KJ804876	KJ804681			KJ805274
Hydnophytum moseleyanum	Malesia	Nepokroeff et al. 1999	AF034913				
Hydnophytum moseleyanum	Papua New Guinea	Andersson 2002					AF410687
Hydnophytum sp.	Australia	Barrabé et al. 2014	KF675912	KF675798	KF676266		KF676088
Hydnophytum sp.	Malesia	Nepokroeff et al. 1999	AF034914				

Myrmecodia armata	Malesia	Nepokroeff et al. 1999	AF034917				
Myrmecodia beccarii	Australia	Chomicki and Renner 2016	KU586347	KU586366			
Myrmecodia dahlii	Papua New Guinea	Chomicki and Renner 2016	KU586348	KU586367			
Myrmecodia horrida	Malesia	Nepokroeff et al. 1999	AF071988				
Myrmecodia horrida	Papua New Guinea	Andersson 2002					AF410690
Myrmecodia platyrea	Malesia	Nepokroeff et al. 1999	AF034918				
Myrmecodia salomonensis	Solomons	Chomicki and Renner 2016	KU586351	KU586370			
Myrmecodia tuberosa	Unknown	Andersson 2002	AF149313				AF000950
Myrmecodia tuberosa	Papua New Guinea	Barrabé et al. 2014	KF675913	KF675799	KF676267		KF676089
		Razafimandimbison et al. 2014				KJ805673	
Myrmephytum arfakianum	Papua New Guinea	Chomicki and Renner 2016	KU586352	KU586371			
Myrmephytum beccarii	Philippines	Chomicki and Renner 2016	KU586353	KU586354			
Myrmephytum selebicum	Malesia	Nepokroeff et al. 1999	AF034916				
Myrmephytum selebicum	Unknown	Andersson 2002					AF410691
Psychotria aff. brackenridgei	Fiji	Andersson 2002					AF410698
Psychotria brevicalyx	Fiji	Andersson 2002					AF410699
Psychotria cadigensis	Philippines	Nepokroeff et al. 1999	AF034910				
Psychotria cadigensis	Philippines	Nepokroeff et al. 2003	AY350673	AY350702			
Psychotria cf. araiosantha	Fiji	Barrabé et al. 2014	KF675922	KF675815	KF676276		KF676099
Psychotria cf. confertiloba	Fiji	Barrabé et al. 2014	KF675923	KF675816	KF676277		KF676100
Psychotria cf. impercepta	Fiji	Barrabé et al. 2012	JX155063	KF675817	JX155196		JX155155
Psychotria cf. vaccinioides	Papua New Guinea	Barrabé et al. 2014	KF675924	KF675818	KF676278		KF676101
Psychotria chrysantha	Papua New Guinea	Andersson 2002					AF410704
Psychotria confertiloba	Fiji	Andersson 2002					AF369857
Psychotria decorifolia	Papua New Guinea	Nepokroeff et al. 1999	AF034911				
Psychotria fauriei	Oahu	Nepokroeff et al. 2003	AY350663	AY350692			
Psychotria fitzalanii	Australia	Nepokroeff et al. 1999	AF072024				
Psychotria grandiflora	Kauai	Andersson 2002					AF410716
Psychotria grandiflora	Kauai	Nepokroeff et al. 2003	AY350670	AY350699			
Psychotria greenwelliae	Kauai	Andersson 2002					AF410746
Psychotria greenwelliae	Kauai	Nepokroeff et al. 2003	AY350665	AY350694			
Psychotria greenwelliae	Kauai	Nepokroeff et al. 2003	AY350666	AY350695			
Psychotria gyrulosa	Borneo	Andersson 2002					AF410718
Psychotria hathewayi	Oahu	Andersson 2002					AF410719

Psychotria hathewayi	Oahu	Nepokroeff et al. 2003	AY350664	AY350693			
Psychotria hawaiiensis	Hawaii	Nepokroeff et al. 2003	AY350659	AY350688			
Psychotria hawaiiensis	Maui	Nepokroeff et al. 2003	AY350660	AY350689			
Psychotria hawaiiensis	Hawaii	Barrabé et al. 2014	KF675941	KF675840	KF676296		KF676116
Psychotria hexandra	Kauai	Nepokroeff et al. 1999	AF034907				
Psychotria hexandra	Kauai	Nepokroeff et al. 2003	AY350667	AY350697			
Psychotria hexandra	Kauai	Nepokroeff et al. 2003	AY350668	AY350696			
Psychotria hexandra var. oahuensis	Oahu	Nepokroeff et al. 2003	AY350669	AY350698			
Psychotria hivaoana	French Polynesia	Barrabé et al. 2014	KF675942	KF675841	KF676297		KF676117
Psychotria hobdyi	Kauai	Nepokroeff et al. 1999	AF034906				
Psychotria hobdyi	Kauai	Nepokroeff et al. 2003	AY350671	AY350700			
Psychotria hombroniana	Kosrae	Nepokroeff et al. 2003	AY350676	AY350705			
Psychotria insularum	Samoa	Andersson 2002	AF149388				AF410724
Psychotria insularum	Wallis & Futuna	Barrabé et al. 2014	KF675843	KF675842	KF676298		KF676118
Psychotria insularum	Samoa	Nepokroeff et al. 1999	AF072056				
Psychotria iteophylla	Borneo	Barrabé et al. 2014					AF410726
Psychotria kaduana	Hawaiian Islands	Andersson 2002	AF149389				AF001351
Psychotria kaduana	Maui	Nepokroeff et al. 2003	AY350657	AY360686			
Psychotria kaduana	Oahu	Nepokroeff et al. 2003	AY350658	AY350687			
Psychotria loniceroides	Australia	Nepokroeff et al. 1999	AF072034				
Psychotria luzoniensis	Philippines	Nepokroeff et al. 2003	AY350674	AY350703			
Psychotria mariana	Mariana	Andersson 2002					AF147570
Psychotria mariana	Tinian Island	Nepokroeff et al. 2003	AY350677	AY350706			
Psychotria mariniana	Kauai	Nepokroeff et al. 1999	AF034904				AF001354
		Razafimandimbison et al. 2014				AJ002185	
Psychotria mariniana	Hawaiian Islands	Andersson 2002					AF001354
Psychotria mariniana	Kauai	Nepokroeff et al. 1999	AF034904				
Psychotria mariniana	Kauai	Nepokroeff et al. 2003	AY350651	AY350680			
Psychotria mariniana	Oahu	Nepokroeff et al. 2003	AY350652	AY350681			
Psychotria mariniana	Oahu	Nepokroeff et al. 2003	AY350653	AY350682			
Psychotria mariniana	Maui	Nepokroeff et al. 2003	AY350654	AY350683			
Psychotria mariniana	Molokai	Nepokroeff et al. 2003	AY350655	AY350684			
Psychotria mariniana	Lanai	Nepokroeff et al. 2003	AY350656	AY350685			

Psychotria mauiensis	Maui	Nepokroeff et al. 2003	AY350661	AY350690			
Psychotria mauiensis	Molokai	Nepokroeff et al. 2003	AY350662	AY350691			
Psychotria membranacea	Philippines	Nepokroeff et al. 1999	AF034909				
Psychotria micralabastra	Papua New Guinea	Barrabé et al. 2014	KF675949	KF675851	KF676304		KF676124
Psychotria micralabastra	Papua New Guinea	Razafimandimbison et al. 2014	KJ804924	KJ804729			AJ320084
Psychotria milnei	Vanuatu	Barrabé et al. 2014	KF675952	KF675854	KF676307		KF676127
Psychotria pickeringii	Fiji	Nepokroeff et al. 2003	AY350679	AY350708			
Psychotria pritchardii	Fiji	Barrabé et al. 2014	KF675992	KF675903	KF676347		KF676165
Psychotria ramuensis	Papua New Guinea	Razafimandimbison et al. 2014	KJ804937	KJ804739		AJ318455	AJ320086
Psychotria rhombocarpa	Kosrae	Razafimandimbison et al. 2014	AF072031				
Psychotria raivavaensis	French Polynesia	Barrabé et al. 2014	KF675960		KF676314		KF676135
Psychotria rubra	Asia	Nepokroeff et al. 1999	AF072035				
Psychotria serpens	Hong Kong	Nepokroeff et al. 1999	AF072036				
Psychotria simmondsiana	Australia	Nepokroeff et al. 1999	AF072022				
Psychotria sp. Guam 1	Guam	Nepokroeff et al. 1999	AF072026				
Psychotria sp. Guam 2	Guam	Nepokroeff et al. 1999	AF072028				
Psychotria sp. Guam 3	Guam	Nepokroeff et al. 1999	AF072033				
Psychotria sp. Guam 4	Guam	Nepokroeff et al. 1999	AF072039				
Psychotria sp.	Tahiti	Nepokroeff et al. 1999	AF072030				
Psychotria sp.	Fiji	Andersson 2002					AF410768
Psychotria sp.	Fiji	Nepokroeff et al. 2003	AY350678	AY350707			
Psychotria sp.	Fiji	Barrabé et al. 2014	KF675967	KF675877	KF676322		KF676142
Psychotria sp.	Vanuatu	Barrabé et al. 2014	KF675971	KF675881	KF676326		KF676146
Psychotria sp.	Fiji	Barrabé et al. 2014	KF675973	KF675884	KF676328		KF676147
Psychotria sp.	Vanuatu	Barrabé et al. 2014	KF675976	KF675887	KF676331		KF676150
Psychotria sp.	Papua New Guinea	Barrabé et al. 2014	KF675986	KF675897	KF676341		KF676160
Psychotria submontana	Australia	Nepokroeff et al. 1999	AF072023				
Psychotria tahitiensis	Tahiti	Nepokroeff et al. 2003	AY350675	AY350704			
Psychotria temehaniensis	French Polynesia	Barrabé et al. 2014	KF675989	KF675900	KF676344		KF676162
Psychotria turbinata	Fiji	Andersson 2002					AF410760
Psychotria unicarinata	Fiji	Andersson 2002					AF410761
Psychotria wawrae	Kauai	Nepokroeff et al. 1999	AF034908				
Psychotria wawrae	Kauai	Nepokroeff et al. 2003	AY350672	AY350701			

Squamellaria grayi	Fiji	Chomicki and Renner 2016	KU586339	KU586358		KU586436
Squamellaria grayi	Fiji	Chomicki and Renner 2016				KU586432
Squamellaria guppyana	Solomons	Chomicki and Renner 2016	KU586345			
Squamellaria huxleyana	Fiji	Chomicki and Renner 2016	KU586336	KU586355		KU586433
Squamellaria imberbis	Fiji	Andersson 2002				AF003620
Squamellaria imberbis	Fiji	Barrabé et al. 2012	KF675993	KF675905	KF676348	KF676166
Squamellaria imberbis	Fiji	Chomicki and Renner 2016	KU586337	KU586356		KU586434
Squamellaria jebbiana	Fiji	Chomicki and Renner 2016	KU586342	KU586361		KU586438
Squamellaria kajewskii	Solomons	Chomicki and Renner 2016	KU586335			
Squamellaria major	Fiji	Chomicki and Renner 2016	KU586338	KU586357		KU586435
Squamellaria tenuiflora	Fiji	Chomicki and Renner 2016				KU586440
Squamellaria tenuiflora	Fiji	Chomicki and Renner 2016	KU586343	KU586362		
Squamellaria thekii	Fiji	Chomicki and Renner 2016	KU586340	KU586359		KU586437
Squamellaria wilkinsonii	Fiji	Chomicki and Renner 2016				KU586439
Squamellaria wilkinsonii	Fiji	Chomicki and Renner 2016		KU586364		
Squamellaria wilkinsonii	Fiji	Chomicki and Renner 2016	KU586344	KU586363		KU586441
Squamellaria wilsonii	Fiji	Chomicki and Renner 2016	KU586341	KU586360		
Streblosa aff. myriocarpa	Borneo	Andersson 2002				AF003621

Table 4. *Psychotria* species outgroups from GenBank used for study, listing the GenBank accession number and the reference in which the sequence was originally published.

Taxon	Reference	*ITS*	*ETS*	*matK-kim*	*psbA*	*rbcL*	*rps16*
Geophila repens	Andersson 2001						AF369846
	Barrabé et al. 2012	JX155079			JX155210		
	Yang et al. 2016			KX911172		KX910856	
Margaritopsis boliviana	Barrabé et al. 2012	JX155097			JX155220	JX155186	
						JX155187	
Notopleura uliginosa	Andersson 2001						AF147581
	Barrabé et al. 2012	AF071991					
	Yang et al. 2016					JQ593717	
Palicourea guianensis	Andersson and Taylor 1999						AF147532
	Kress et al. 2009			GQ982058	GQ982311	GQ981825	
	Nepokroeff et al. 1999	AF072010					
	Razafimandimbison et al. 2014		KJ804678				
Psychtoria flava	Barrabé et al. 2014		KF675833				KF6766111
	Paul et al. 2008	FJ208600			FJ208661		
Psychotria grandis	Barrabé et al. 2012	JX155080				JQ593774	
	Barrabé et al. 2014		KF675839				
	Kress et al. 2009			GQ982078	GQ982341		
	Unpublished						JX155171
Psychotria mapourioides	Baraloto et al. 2012			JQ626482		JQ626079	
	Barrabé et al. 2012				KF676303		
	Barrabé et al. 2014	KF675948	KF675850				KF676123
Psychotria poeppiginana	Andersson and Taylor 1999						AF147539
	Nepokroeff et al. 1999	AF071993					
	Razafimandimbison et al. 2014					KJ805730	
	Unpublished			JQ598009			
Psychotria samoana	Barrabé et al. 2012	JX155091			JX155221		JX155180
	Barrabé et al. 2014		KF675866				
Psychotria trichotoma	Andersson 2002						AF410759
	Paul et al. 2008	FJ208639			FJ208693		

Rudgea stipulacea	Barrabé et al. 2012 Barrabé et al. 2014	JX155099	KF675904	JX155226	JX155189

Table 5. Nuclear ribosomal and chloroplast markers used in study.

Locus	Primer Sequence (5'→3')	Reference
Nuclear Ribosomal Genome		
ITS	F: GTCCACTGAACCTTATCATTTAG	Dong et al. 2013
	R: TCCTCCGCTTATTGATATGC	Dong et al. 2013
ETS	F: GCAGGATCAACCAGGTAGCA	Nepokroeff et al. 2003
	R: GTGTGAGTGGTAAATGGATAGC	Nepokroeff et al. 2003
Chloroplast Genome		
matK-kim	F: CGTACAGTACTTTTGTGTTTACGAG	Kress et al. 2005
	R: ACCCAGTCCATCTGGAAATCTTGGTTC	Kress et al. 2005
psbA	F: GTTATGCATGAACGTAATGCTC	Kress et al. 2005
	R: CGCGCATGGTGGATTCACAATCC	Kress et al. 2005
psbE-petL	F: GGTGCTGACGAATAGCCAAC	Dong et al. 2013
	R: GAGGTTATAGTTAAAGCTGC	Dong et al. 2013
rbcL	F: ATGTCACCACAAACAGAAACTAAAGC	Bremer et al. 2002
	R: CTTTTAGTAAAAGATTGGGCCGAG	Bremer et al. 2002
rps16	F: GTGGTAGAAAGCAACGTGCGACTT	Dong et al. 2013
	R: TCGGGATCGAACATCAATTGCAAC	Dong et al. 2013
trnK-rps16	F: AAAGCCGAGTACTCTACCGTTG	Dong et al. 2013
	R: ATTGATGTTCGATCCCGAAG	Dong et al. 2013
trnT-psbD	F: TCGGTTCAAATCCGATAAGG	Dong et al. 2013
	R: GTCCCTACGTAACCAGTCAT	Dong et al. 2013

Table 6. Characteristics of nuclear and chloroplast loci genomes used for inferring phylogenies.

Markers	Aligned Sequence Length (bp)	# of constant sites	# of variable sites (parsimony-uninformative and parsimony-informative)	# of parsimony-informative sites
ITS	670	408	262	217
ETS	433	199	234	185
matK	764	595	169	55
psbA	587	433	154	110
psbE-petL	1112	896	216	78
rbcL	568	531	37	31
rps16	969	824	145	97
trnK-rps16	1150	888	262	140
trnT-psbD	1548	1212	336	139

Table 7. Concatenated alignments used in study to infer phylogenies of Hawaiian and South Pacific *Psychotria.*

Alignment	Markers within alignment	Aligned sequence length (bp)	# of constant sites	# of variable sites (parsimony-uninformative and parsimony-informative)	# of parsimony-informative sites	# of tips
8-Loci	ITS, ETS, psbA, psbE, rbcL, rps16, trnK, trnT	7037	5391	1646	997	109
6-Loci	ITS, ETS, matK, psbA, rbcL, rps16	4245	2701	1544	968	199
3-Loci	ITS, ETS, rps16	2244	801	1443	867	273
Chloroplast Loci	psbA, psbE, rbcL, rps16, trnK, trnT	5934	4784	1150	595	109

Table 8. Occurrence data of Hawaiian *Psychotria* species. Data obtained from the Global Biodiversity Information Facility (GBIF) database, accessed on 1/12/16; as well as the National Tropical Botanical Garden (NTBG) database, and from our collaborator Dr. Kenta Watanabe of the Okinawa National College of Technology in Japan. Coordinates withheld for *P. grandiflora, P. hobdyi,* and *P. hexandra var. oahuensis* by the Plant Extinction Prevention Plan (PPEP) are not shown.

Species	**Latitude**	**Longitude**
Psychotria fauriei	21.32476	-157.74339
Psychotria fauriei	21.32446	-157.74214
Psychotria fauriei	21.32305	-157.7289
Psychotria fauriei	21.32307	-157.72888
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria grandiflora	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria greenwelliae	22.09020042	-159.6152496
Psychotria greenwelliae	22.1461	-159.63586
Psychotria greenwelliae	22.13333	-159.63333
Psychotria greenwelliae	22.08	-159.61999
Psychotria greenwelliae	22.1667	-159.633
Psychotria greenwelliae	22.1628	-159.633
Psychotria greenwelliae	22.13515663	-159.6826935
Psychotria greenwelliae	22.10808754	-159.6571503
Psychotria greenwelliae	22.08503914	-159.6296844
Psychotria greenwelliae	22.16166667	-159.6394444
Psychotria greenwelliae	22.14364052	-159.6564026
Psychotria greenwelliae	22.08333333	-159.6666666
Psychotria greenwelliae	22.11805556	-159.6152777
Psychotria greenwelliae	22.14611111	-159.6586111
Psychotria hathewayi	21.46667	-157.98333
Psychotria hathewayi	21.4167	-158.1
Psychotria hathewayi	21.46083	-158.20166

Psychotria hathewayi	21.425171	-158.090454
Psychotria hathewayi	21.53234	-158.1793
Psychotria hathewayi	21.53251	-158.17831
Psychotria hathewayi	21.41264916	-158.1005096
Psychotria hathewayi	21.41242	-158.099976
Psychotria hawaiiensis	19.45	-154.867
Psychotria hawaiiensis	19.62	-155.12
Psychotria hawaiiensis	19.6	-155.1
Psychotria hawaiiensis	19.5333	-154.85
Psychotria hawaiiensis	19.5167	-154.867
Psychotria hawaiiensis	20.7206	-156.018
Psychotria hawaiiensis	20.7433	-156.013
Psychotria hawaiiensis	19.5	-155
Psychotria hawaiiensis	19.9333	-155.283
Psychotria hawaiiensis	19.0833	-155.617
Psychotria hawaiiensis	19.5	-155.317
Psychotria hawaiiensis	19.5167	-155.833
Psychotria hawaiiensis	19.5333	-154.85
Psychotria hawaiiensis	19.5	-155.3
Psychotria hawaiiensis	19.5167	-154.867
Psychotria hawaiiensis	20.72	-156.02
Psychotria hawaiiensis	19.45	-155.867
Psychotria hawaiiensis	19.6167	-155.117
Psychotria hawaiiensis	19.0667	-155.633
Psychotria hawaiiensis	19.4833	-155.317
Psychotria hawaiiensis	20.75	-156.017
Psychotria hawaiiensis	19.43966	-155.30261
Psychotria hawaiiensis	19.4421	-155.30161
Psychotria hawaiiensis	19.4386	-155.30282
Psychotria hawaiiensis	19.43969	-155.30254
Psychotria hawaiiensis	19.5	-155.6
Psychotria hexandra	22.14	-159.69
Psychotria hexandra	22.1172	-159.67206
Psychotria hexandra	22.12004	-159.60304
Psychotria hexandra	22.13333	-159.61667
Psychotria hexandra	22.10283089	-159.6295013

Psychotria hexandra	22.14598084	-159.6934052
Psychotria hexandra	22.15135002	-159.6575012
Psychotria hexandra	22.12043	-159.603043
Psychotria hexandra	22.18562317	-159.5791931
Psychotria hexandra	22.20194444	-159.5811111
Psychotria hexandra	22.14611111	-159.6586111
Psychotria hexandra	22.13333333	-159.6166666
Psychotria hexandra	22.14072037	-159.6575928
Psychotria hexandra	22.033344	-159.499313
Psychotria hexandra	22.188643	-159.578461
Psychotria hexandra	22.11720085	-159.6720581
Psychotria hexandra	22.18694444	-159.5827777
Psychotria hexandra	22.1	-159.5
Psychotria hexandra var oahuensis	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hexandra var oahuensis	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hexandra var oahuensis	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hexandra var oahuensis	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria hobdyi	Withheld request by the PPEP	Withheld request by the PPEP
Psychotria kaduana	21.3475	-157.86222
Psychotria kaduana	21.6	-157.9
Psychotria kaduana	21.7	-158
Psychotria kaduana	21.4333	-157.9667

Psychotria kaduana	21.32	-157.8
Psychotria kaduana	22.19	-159.60001
Psychotria kaduana	22.1617	-159.6431
Psychotria kaduana	22.1667	-159.633
Psychotria kaduana	22.19024086	-159.6031036
Psychotria kaduana	20.87327957	-156.6191864
Psychotria kaduana	20.87342072	-156.6191406
Psychotria kaduana	20.84055556	-156.5519444
Psychotria kaduana	22.1	-159.5
Psychotria kaduana	21.31905	-157.72978
Psychotria kaduana	21.3209	-157.73011
Psychotria kaduana	21.33823	-157.81088
Psychotria kaduana	21.46134	-158.09944
Psychotria kaduana	21.33535	-157.81075
Psychotria mariniana	21.8917	-159.508
Psychotria mariniana	22.1833	-159.583
Psychotria mariniana	21.32	-157.8
Psychotria mariniana	21.16339	-156.90483
Psychotria mariniana	22.21161842	-159.5826721
Psychotria mariniana	22.2	-159.6
Psychotria mariniana	22.195	-159.5972
Psychotria mariniana	22.0664	-159.484
Psychotria mariniana	22.2103	-159.5831
Psychotria mariniana	22.10861111	-159.5913888
Psychotria mariniana	21.32	-157.8
Psychotria mariniana	20.8333	-156.217
Psychotria mariniana	22.157822	-159.640366
Psychotria mariniana	22.2025	-159.6061111
Psychotria mariniana	21.16333333	-156.9047222
Psychotria mariniana	21.65277778	-157.9177777
Psychotria mariniana	19.28138889	-155.8622222
Psychotria mariniana	22.19762993	-159.5969543
Psychotria mariniana	21.453939	-157.882629
Psychotria mariniana	22.12043	-159.603043
Psychotria mariniana	21.984	-159.34515
Psychotria mariniana	21.92953301	-159.4176178

Psychotria mariniana	22.19833333	-159.5755555
Psychotria mariniana	22.18944444	-159.5830555
Psychotria mariniana	22.21027778	-159.5830555
Psychotria mariniana	22.20055556	-159.5838888
Psychotria mariniana	22.19222222	-159.5858333
Psychotria mariniana	21.51583333	-157.9247222
Psychotria mariniana	21.1	-156.9
Psychotria mariniana	22.06638889	-159.4836111
Psychotria mariniana	20.852392	-156.575897
Psychotria mariniana	21.53475	-158.18133
Psychotria mariniana	21.12408	-156.91751
Psychotria mariniana	21.12792	-156.91932
Psychotria mariniana	21.31635	-157.72961
Psychotria mariniana	19.36058	-155.168813
Psychotria mauiensis	20.68	-156.1014
Psychotria mauiensis	21.3228	-157.7408
Psychotria mauiensis	21.1	-156.883
Psychotria mauiensis	22.049999	-159.490005
Psychotria mauiensis	20.874465	-156.619772
Psychotria mauiensis	22.048477	-159.48735
Psychotria mauiensis	21.16166667	-156.9025
Psychotria mauiensis	20.742001	-156.048508
Psychotria mauiensis	20.70416667	-156.1013888
Psychotria mauiensis	20.73141	-156.065885
Psychotria mauiensis	20.867658	-156.606887
Psychotria mauiensis	21.11909	-156.89965
Psychotria mauiensis	21.12549	-156.90162
Psychotria mauiensis	21.12571	-156.8998
Psychotria mauiensis	21.1252	-156.89795
Psychotria mauiensis	21.12524	-156.89813
Psychotria mauiensis	21.11953	-156.89963
Psychotria wawrae	22.12	-159.4483
Psychotria wawrae	22.1095295	-159.3935547
Psychotria wawrae	22.116308	-159.396118
Psychotria wawrae	22.15	-159.4166666
Psychotria wawrae	22.13666667	-159.4483333

Psychotria wawrae	22.1086	-159.39052
Psychotria wawrae	22.1095	-159.39213
Psychotria wawrae	22.10956	-159.39217
Psychotria wawrae	22.1535	-159.3388
Psychotria wawrae	22.15354	-159.33695
Psychotria wawrae	22.1535	-159.3388

Table 9. Global Climatic Data obtained from WorldClim. All 19 Bioclim variables were used in the analysis of raw climate plots. The specific variables used in MaxEnt and ENMTools analysis are in bold.

Bioclim variable	**Variable representation**
Bio1	Annual Mean Temperature
Bio2	**Mean Diurnal Range (Mean of monthly (max temp - min temp))**
Bio3	**Isothermality (Bio2/Bio7 *100)**
Bio4	**Temperature Seasonality (Standard deviation * 100)**
Bio5	Max Temperature of Warmest Month
Bio6	Min Temperature of Coldest Month
Bio7	**Temperature Annual Range (Bio5 - Bio6)**
Bio8	Mean Temperature of Wettest Quarter
Bio9	Mean Temperature of Driest Quarter
Bio10	Mean Temperature of Warmest Quarter
Bio11	**Mean Temperature of Coldest Quarter**
Bio12	**Annual Precipitation**
Bio13	Precipitation of Wettest Month
Bio14	Precipitation of Driest Month
Bio15	**Precipitation Seasonality (Coefficient of variation)**
Bio16	Precipitation of Wettest Quarter
Bio17	**Precipitation of Driest Quarter**
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter

Table 10. Divergence times of the Hawaiian *Psychotria.* Median = node age, 95% HPD (L or H) = Highest Posterior Density Distribution (lowest to highest)

Phylogeny	**8-Loci**			**6-Loci**			**3-Loci**			**Chloroplast-Loci**		
	Median	95% HPD L	95% HPD H	Median	95% HPD L	95% HPD H	Median	95% HPD L	95% HPD H	Median	95% HPD L	95% HPD H
Hawaii Crown	8.73	6.08	11.69	7.24	4.79	10.59	8.23	4.97	11	9.21	6.1	12.81
P. hexandra – P.hexandra var oahuensis	2.5	0.9	4.93	2.51	1.08	4.57	3.03	1.04	4.96	1.63	0.57	4.34
P. grandiflora – P. hobdyi	3.51	1.48	6.34	3.45	1.62	5.81	4.51	1.83	6.83	3.83	1.48	7.02
P. mariniana – P. wawrae	4.01	2.12	6.39	3.82	2.17	5.88	4.59	2.42	6.4	5.73	2.92	8.98
P. greenwelliae – P. mariniana	6.33	3.96	8.75	5.35	3.27	7.85	4.05	3.53	8.17	9.21	6.1	12.81

Table 11a. Model statistics from BioGeoBEARS analysis using BEAST Chronogram – Hawaiian and South Pacific *Psychotria*, 6 Loci. *d* = rate of dispersal/range addition; *e* = extinction rate/range contraction; and *j* = rate of founder events. The best model chosen is in bold.

Model	**LnL**	**Number of parameters**	***d***	***e***	***j***
DEC	-70.09	2	0.0052	1.00E-12	0
DEC+J	**-53.44**	**3**	**1.00E-12**	**1.00E-12**	**0.028**
DIVALIKE	-71.76	2	0.0085	2.00E-09	0
DIVALIKE+J	-53.17	3	1.00E-12	1.00E-12	0.029
BAYAREALIKE	-110.2	2	0.007	0.068	0
BAYAREALIKE+J	-55.75	3	1.00E-07	1.00E-07	0.031

Table 11b. Model statistics from BioGeoBEARS analysis using BEAST Chronogram – Hawaiian *Psychotria,* 6 Loci. *d* = rate of dispersal/range addition; *e* = extinction rate/range contraction; and *j* = rate of founder events. The best model chosen is in bold.

Model	**LnL**	**Number of parameters**	***d***	***e***	***j***
DEC	-44.1	2	0.031	1.00E-12	0
DEC+J	**-27.66**	**3**	**1.00E-12**	**1.00E-12**	**0.099**
DIVALIKE	-40.2	2	0.038	1.00E-12	0
DIVALIKE+J	-27.86	3	1.00E-12	1.00E-12	0.098
BAYAREALIKE	-53.55	2	0.028	0.24	0
BAYAREALIKE+J	-27.94	3	1.00E-07	1.00E-07	0.092

Table 12. Niche breadths of Hawaiian *Psychotria*. *P. kaduana* clade consists of *P. fauriei, P. hathewayi, P. hawaiiensis, P. mauiensis.*

Taxon	**Niche breadth (inverse concentration)**	**Uncertainty**
Psychotria fauriei	0.0248	0.6976
Psychotria grandiflora	0.0087	0.5475
Psychotria greenwelliae	0.0351	0.7244
Psychotria hathewayi	0.5172	0.9599
Psychotria hawaiiensis	0.5757	0.9612
Psychotria hexandra	0.0302	0.7044
Psychotria hexandra var oahuensis	0.1527	0.8586
Psychotria hobdyi	0.0982	0.8383
Psychotria kaduana	0.5647	0.9655
Psychotria kaduana clade	0.6493	0.9719
Psychotria mariniana	0.3967	0.9372
Psychotria mauiensis	0.6643	0.9743
Psychotria wawrae	0.0567	0.7576

Table 12. Niche breadths of Hawaiian *Psychotria*. *P. kaduana* clade consists of *P. fauriei, P. hathewayi, P. hawaiiensis,* and *P. mauiensis*.

Taxon	Niche breadth (inverse concentration)	Uncertainty
Psychotria grandiflora	0.0087	0.5475
Psychotria fauriei	0.0248	0.6976
Psychotria hexandra	0.0302	0.7044
Psychotria greenwelliae	0.0351	0.7244
Psychotria wawrae	0.0567	0.7576
Psychotria hobdyi	0.0982	0.8383
Psychotria hexandra var oahuensis	0.1527	0.8586
Psychotria mariniana	0.3967	0.9372
Psychotria hathewayi	0.5172	0.9599
Psychotria kaduana	0.5647	0.9655
Psychotria hawaiiensis	0.5757	0.9612
Psychotria mauiensis	0.6643	0.9743
Psychotria kaduana clade	0.6493	0.9719

Table 13a. Variable loadings from a principal component analyses of 19 bioclimatic variables for the Hawaiian *Psychotria*.

Variable	PC1	PC2
Bio01	-0.0041572	-0.0498716
Bio02	0.0007889	0.0051643
Bio03	-0.0005136	-0.0116931
Bio04	0.0460097	0.8190217
Bio05	-0.0027309	-0.0268527
Bio06	-0.0049182	-0.0576105
Bio07	0.0021873	0.0307578
Bio08	-0.0043615	-0.0576608
Bio09	-0.0046699	-0.0419195
Bio10	-0.0035978	-0.0382765

Bio11	-0.0047375	-0.0600931
Bio12	-0.8985264	-0.0260783
Bio13	-0.0848729	0.1224988
Bio14	-0.0550831	-0.0444991
Bio15	0.0073678	0.0306966
Bio16	-0.2318001	0.3175148
Bio17	-0.2127444	-0.2079057
Bio18	-0.2094141	-0.1883272
Bio19	-0.1930414	0.3365894

Table 13b. Variable loadings from a principal component analyses of 19 bioclimatic variables for South Pacific and Hawaiian *Psychotria*, using species means.

Variable	**PC1**	**PC2**
Bio01	-0.0065259	-0.0135128
Bio02	0.0018732	-0.0074035
Bio03	-0.0068149	-0.0160419
Bio04	0.4380034	0.8911701
Bio05	-0.0001207	-0.0066335
Bio06	-0.0136592	-0.0239636
Bio07	0.0135385	0.0173301
Bio08	-0.0041484	-0.0053532
Bio09	-0.0089721	-0.0196817
Bio10	-0.0011524	-0.0026443
Bio11	-0.0123761	-0.025302
Bio12	-0.8071722	0.3744918
Bio13	-0.0544155	0.055093
Bio14	-0.0615484	0.0201836
Bio15	0.0092149	0.0037902
Bio16	-0.1595976	0.1562325
Bio17	-0.2106314	0.0793948
Bio18	-0.1660845	0.1487154
Bio19	-0.2272801	0.082522

Table 14. Multiple regression statistics, with response to the number of island occupancy. There are two metric of species age, stem age (split from most recent common ancestor), and crown age (earliest divergence within a lineage), the two metrics of niche breadth, and two morphological characters related to dispersal, fruit size and plant height). Significant relationship overall ($P = 0.04$), with plant height being the only significant individual factor; marked in bold.

Factor/Trait	Estimate	Std. Error	t-value	Pr(>|t|)
(Intercept)	6.10E-01	4.39E+00	0.139	0.8949
Stem_age	1.45E-01	5.50E-01	0.264	0.8023
Crown_age	2.89E-01	6.57E-01	0.44	0.6781
Niche_breadth_IC	3.55E+00	3.23E+00	1.101	0.3212
Niche_breadth_U	-2.10E+00	4.88E+00	-0.431	0.6846
Height	**1.66E-04**	**6.81E-05**	**2.43**	**0.0594**
Fruit_long	8.13E-03	1.39E-01	0.058	0.9557
Residual standard error: 0.9363 on 5 degrees of freedom.				
Multiple R-squared: 0.8668, Adjusted R-squared: 0.707				
F-statistic: 5.424 on 6 and 5 DF, p-value: 0.04117				

FIGURES

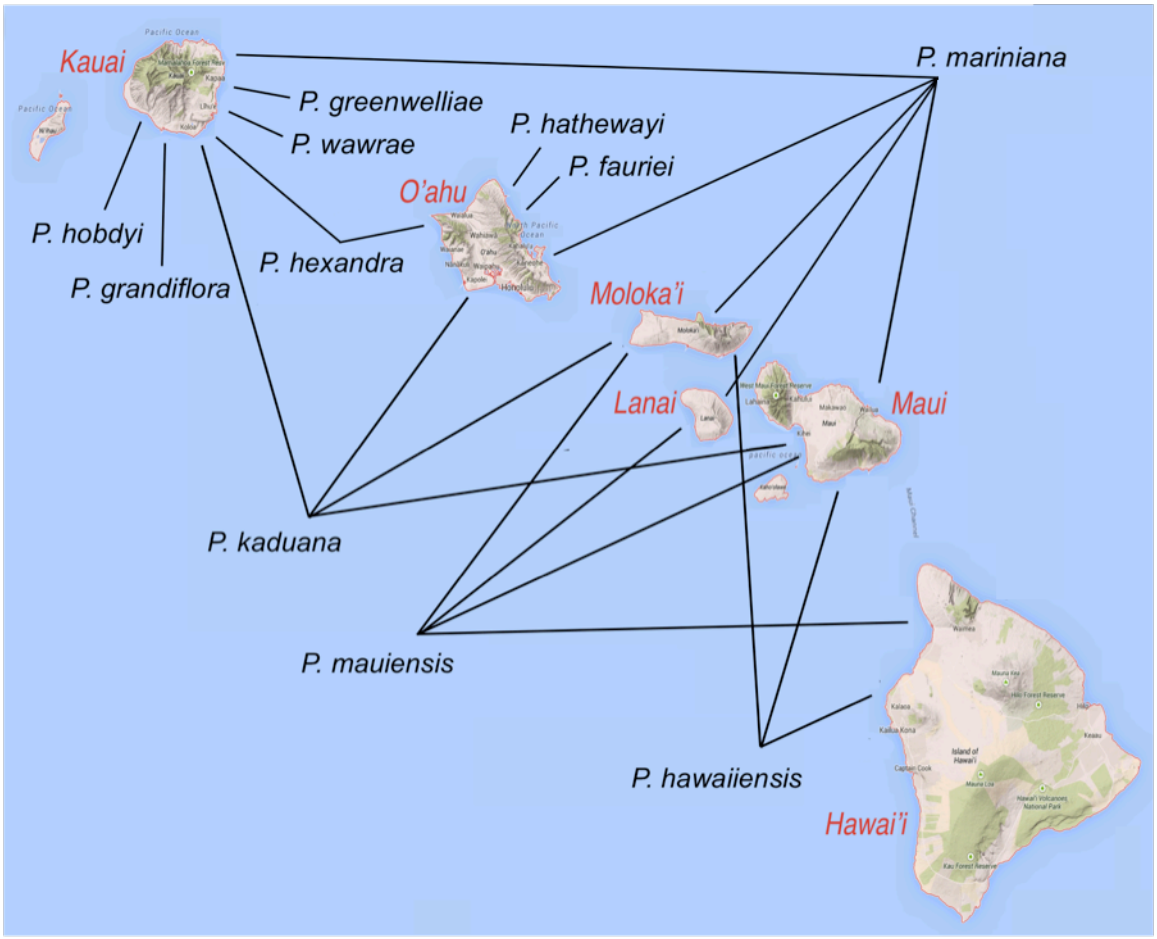


Figure 1. Distribution of Hawaiian *Psychotria* species on the Hawaiian Islands.

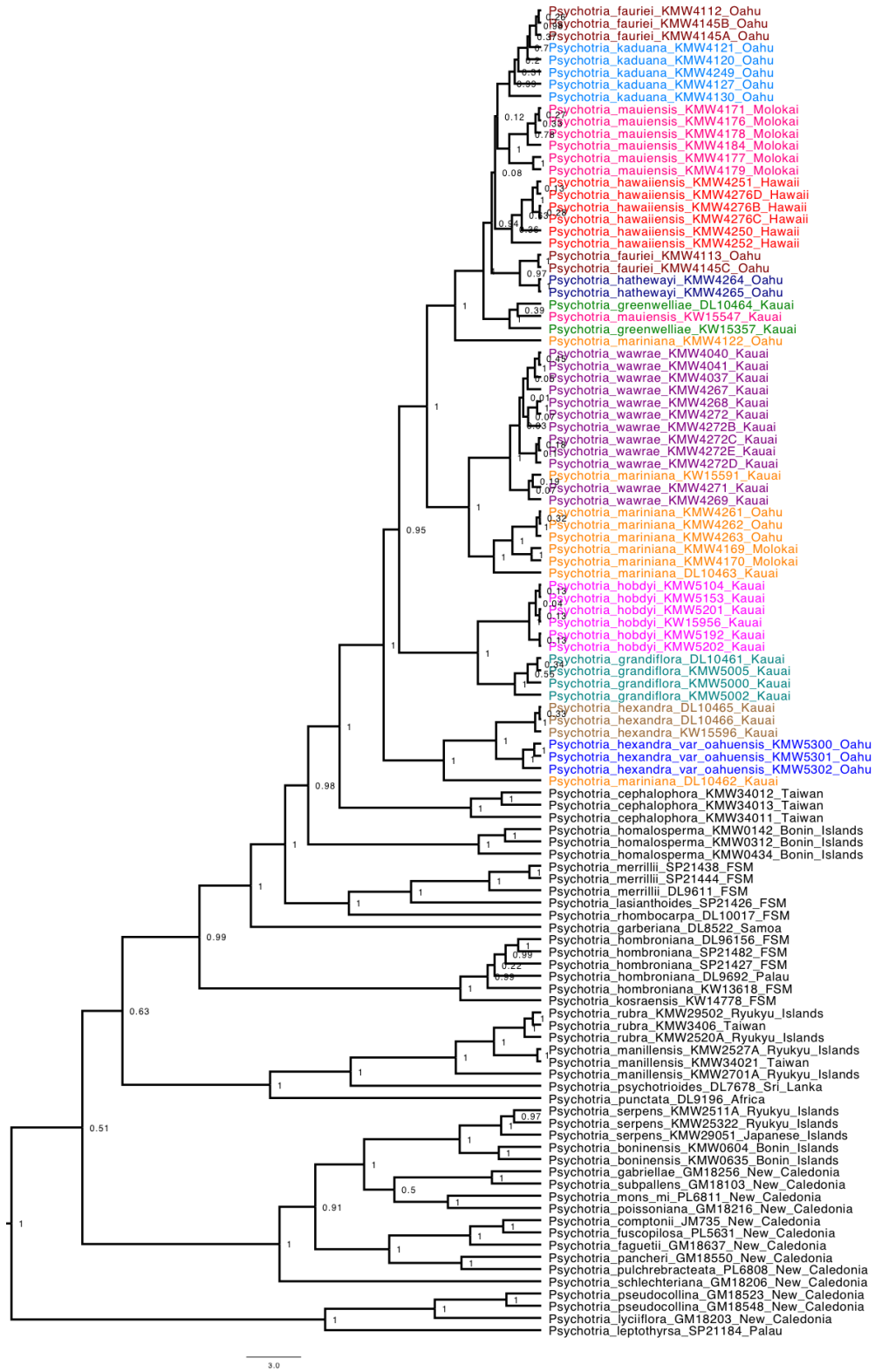


Figure 2a. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 8 loci markers (ITS, ETS, psbA, psbE, rbcL, rps16, tnK, and trnT). Node numbers depict posterior probability of the clades. Species in the Hawaiian clade are color-coded.

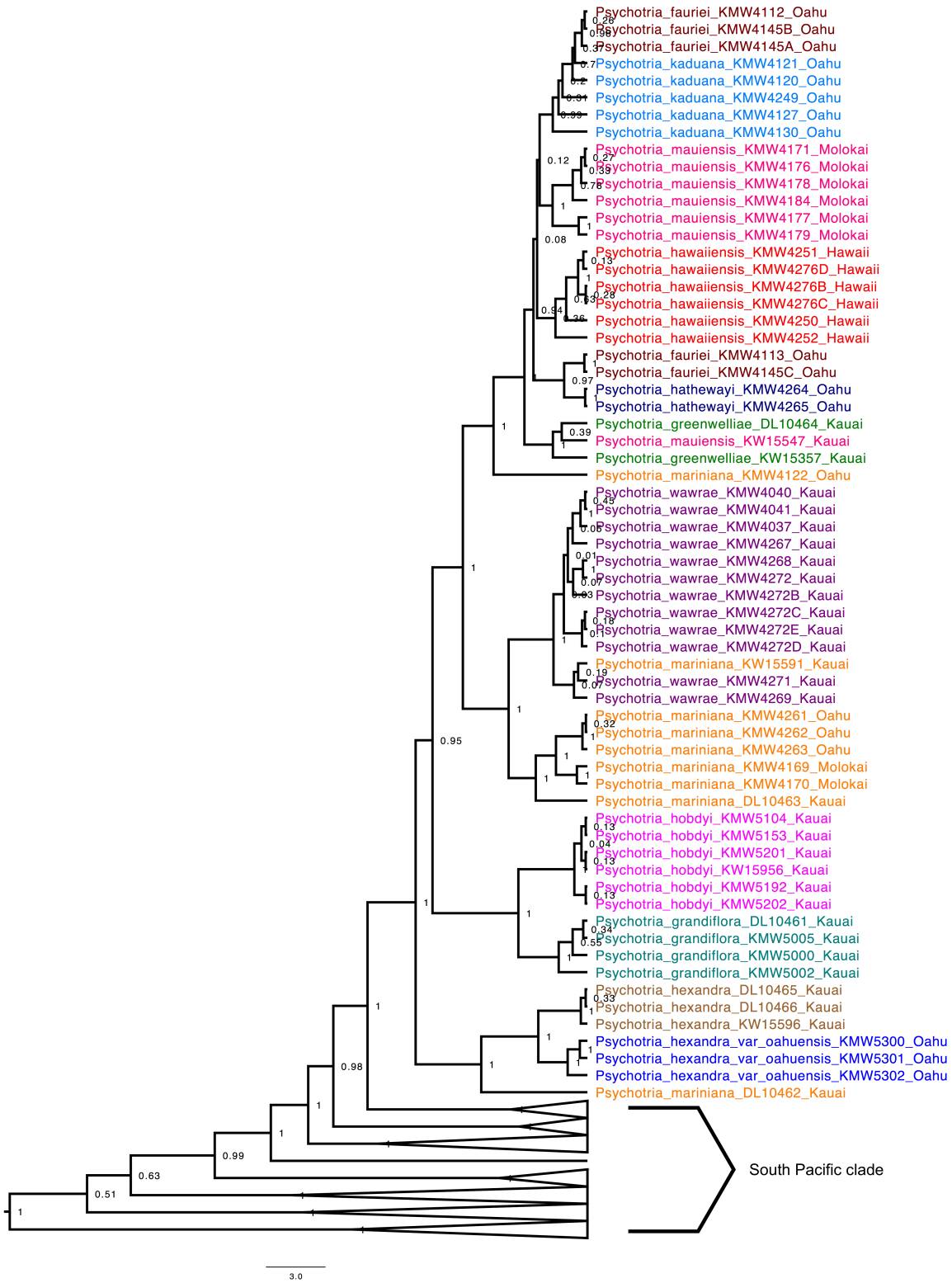


Figure 2b. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 8 loci markers (ITS, ETS, psbA, psbE, rbcL, rps16, tnK, and trnT). Node numbers depict posterior probability of the clades. Each species in the Hawaiian clade is color-coded. The South Pacific clade is collapsed.

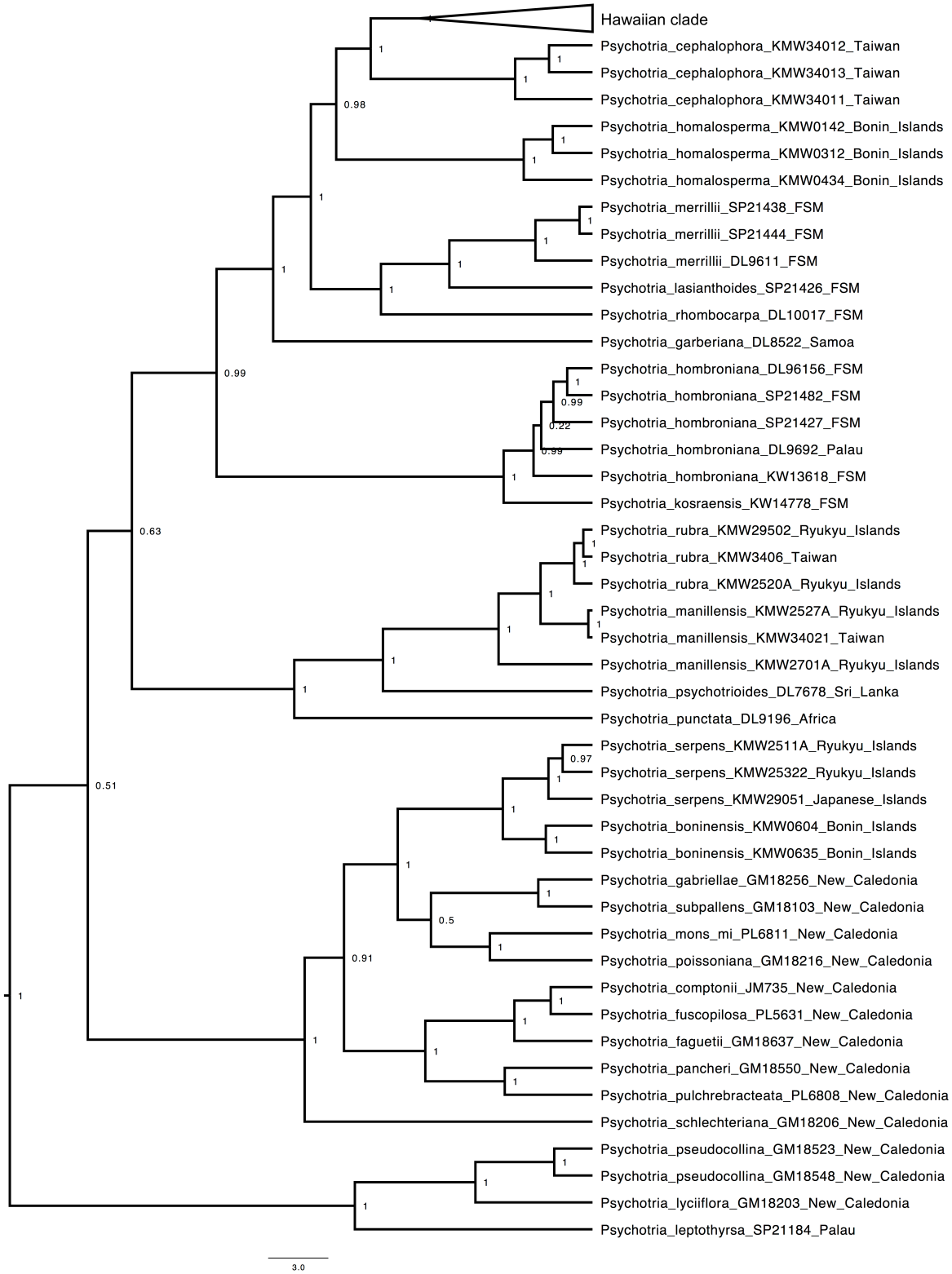


Figure 2c. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 8 loci markers (ITS, ETS, psbA, psbE, rbcL, rps16, tnK, and trnT). Node numbers depict posterior probability of the clades. The South Pacific clade is expanded and the Hawaiian clade is collapsed.

Figure 3a. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, and rps16). Node numbers depict posterior probability of the clades. Species in the Hawaiian clade are color-coded.

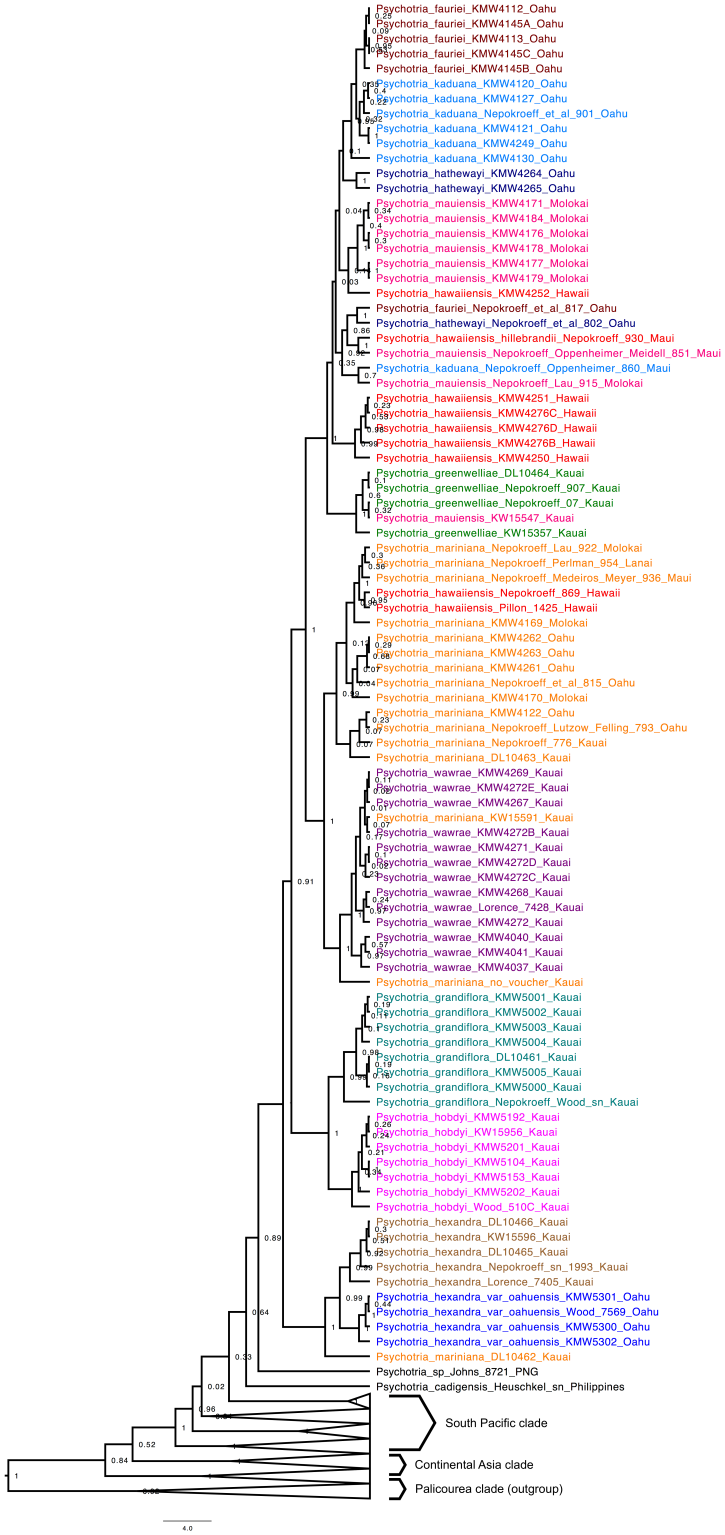


Figure 3b. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, and rps16). Node numbers depict posterior probability of the clades. Each species in the Hawaiian clade is color-coded. The South Pacific clade, Continental Asia clade, and Palicourea clade (outgroup) are collapsed.

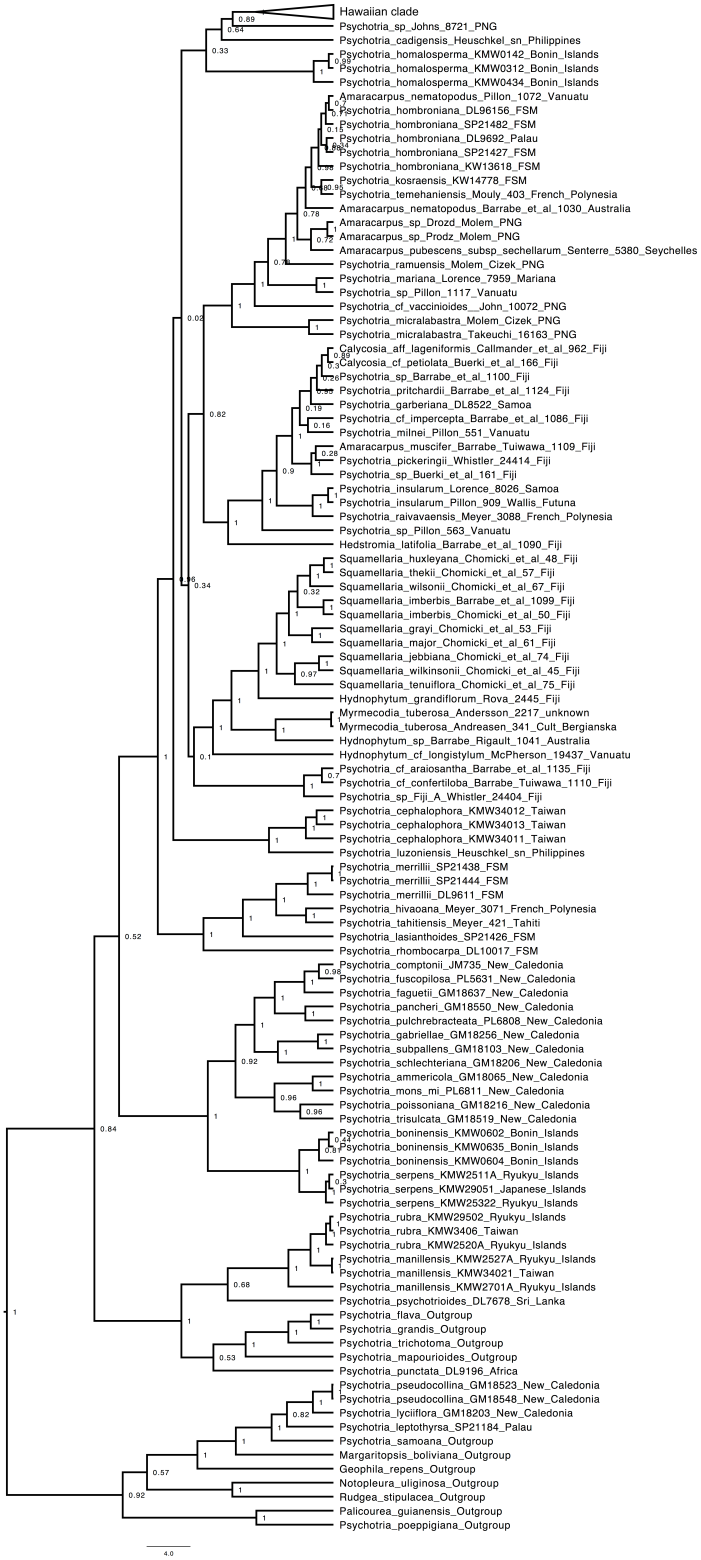


Figure 3c. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, and rps16). Number depicts posterior probability for the clades. The South Pacific clade, Continental Asia clade, and Palicourea clade (outgroup) are expanded and the Hawaiian clade is collapsed.

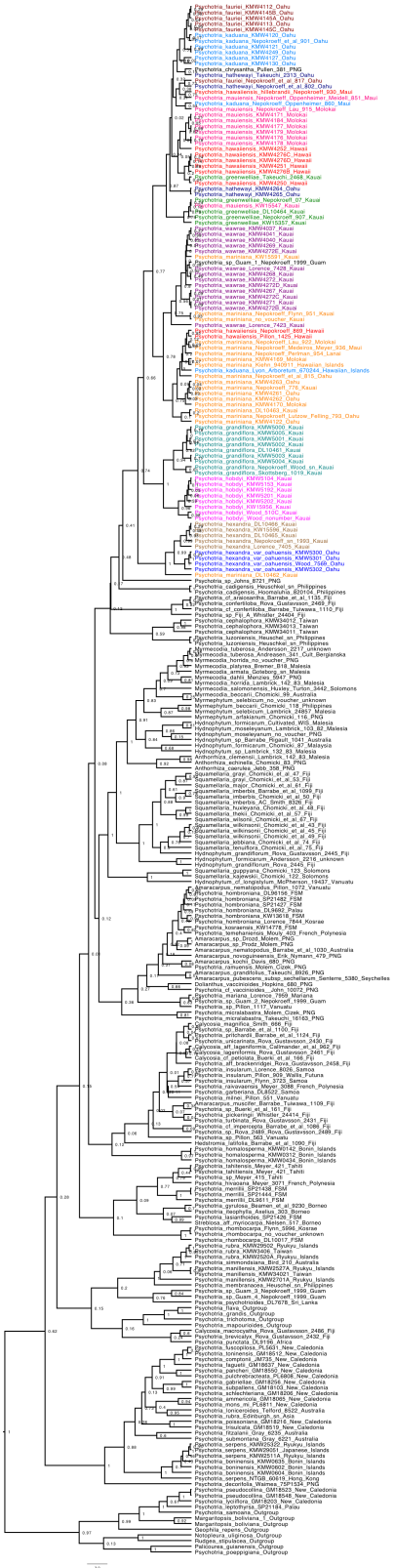


Figure 4a. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 3 loci markers (ITS, ETS, and rps16). Node numbers depict posterior probability of the clades. Species in the Hawaiian clade are color-coded.

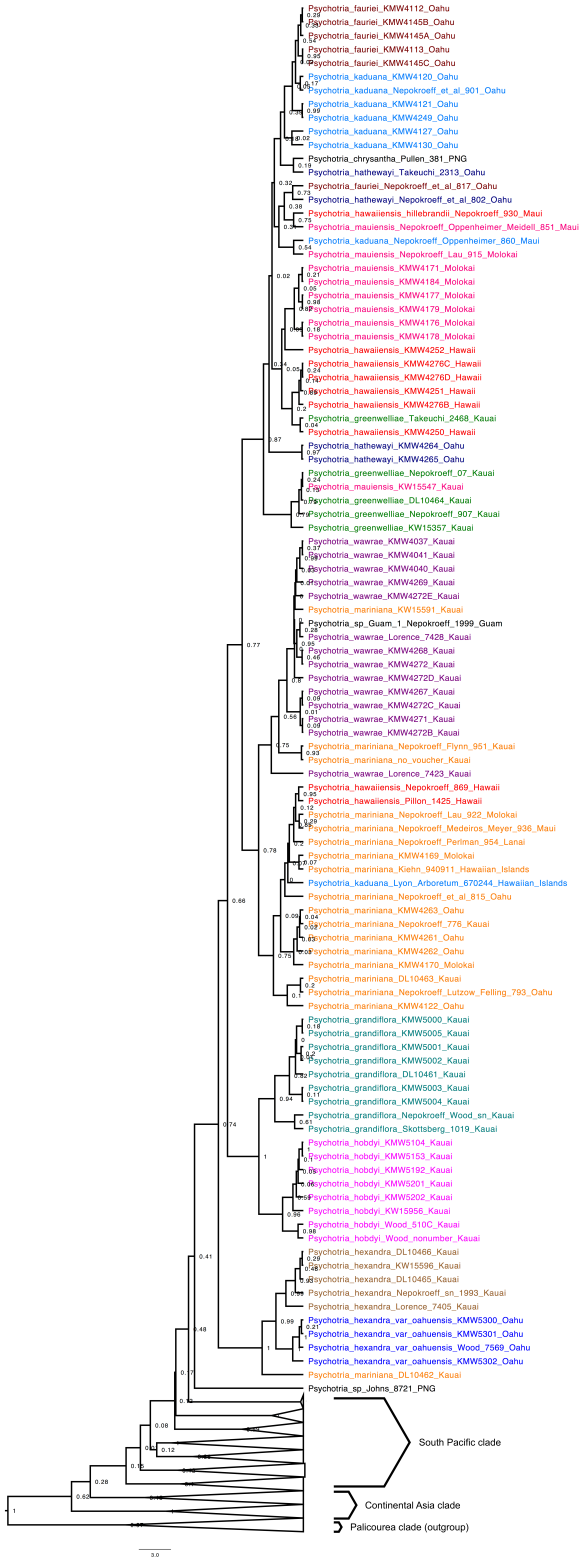


Figure 4b. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 3 loci markers (ITS, ETS, and rps16). Node numbers depict posterior probability of the clades. Each species in the Hawaiian clade is color-coded. The South Pacific clade, Continental Asia clade, and Palicourea clade (outgroup) are collapsed.

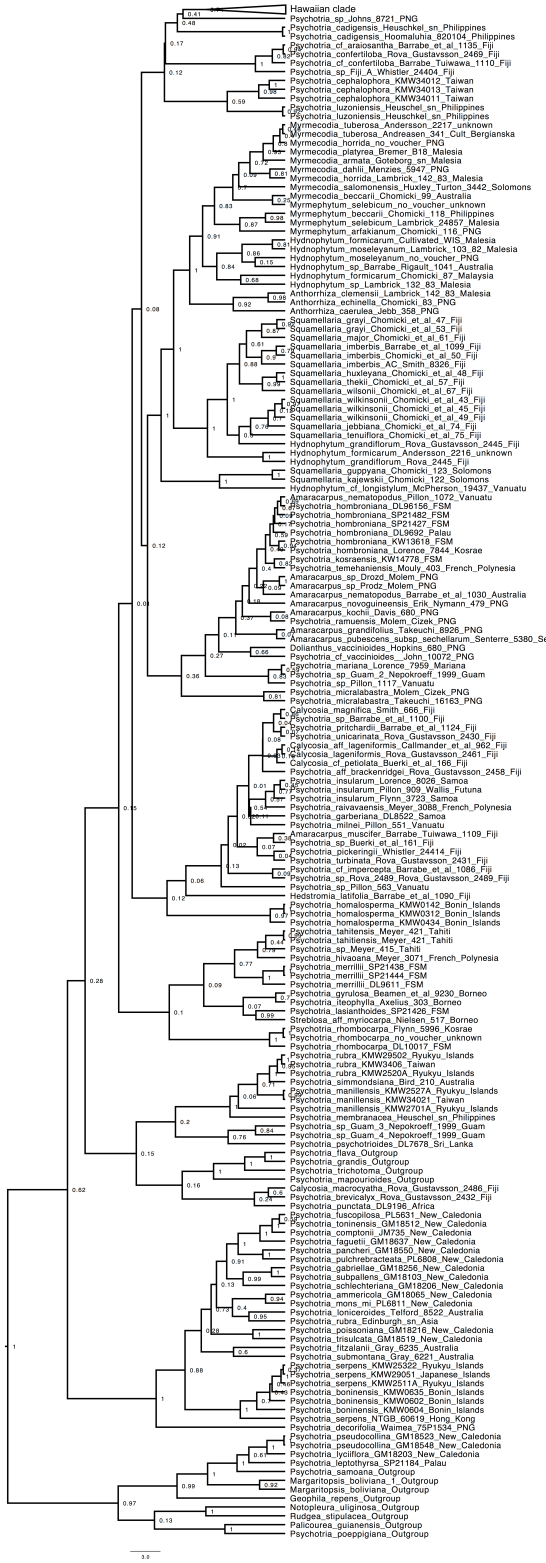


Figure 4c. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 3 loci markers (ITS, ETS, and rps16). Node numbers depict posterior probability of the clades. The South Pacific clade, Continental Asia clade, and Palicourea clade (outgroup) are expanded and the Hawaiian clade is collapsed.

Figure 5a. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, and rps16). Number on the nodes depict range of node ages for the clades represented as the 95% HPD (Low to High) = Highest Posterior Density. Species in the Hawaiian clade are color-coded.

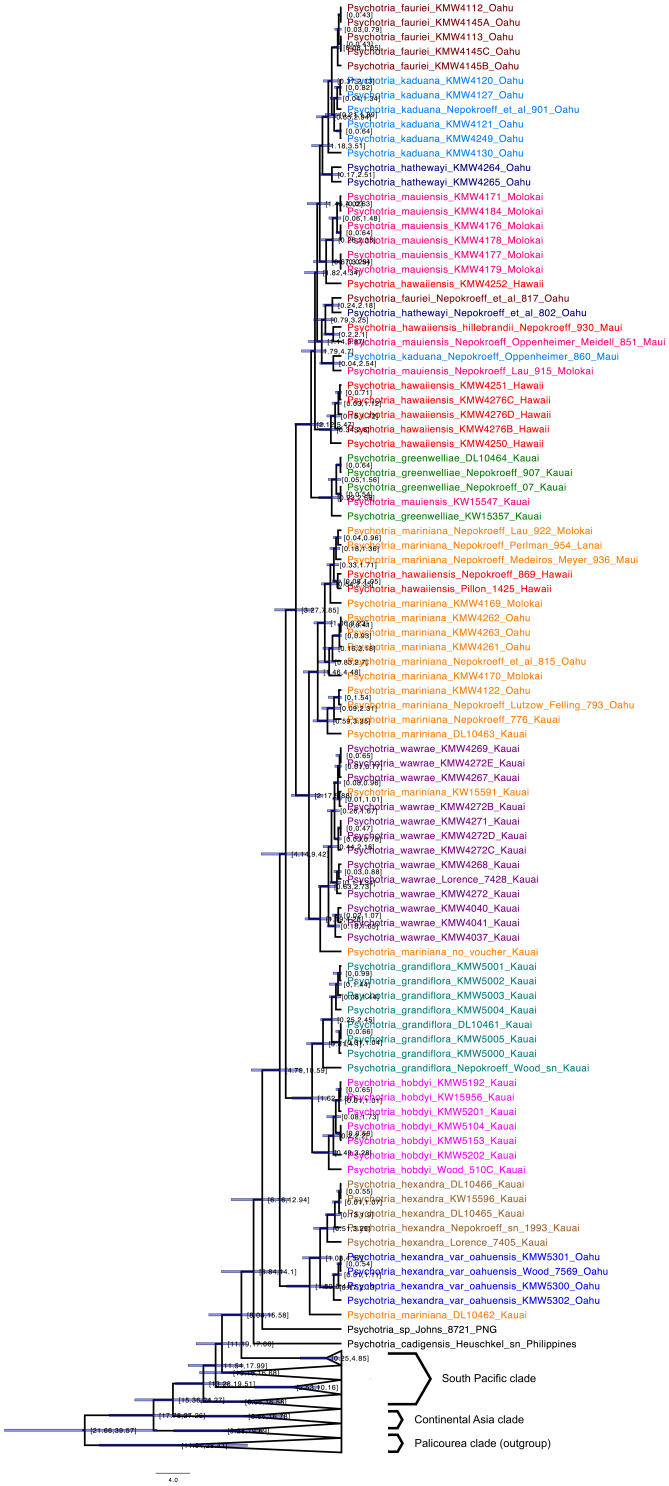


Figure 5b. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, and rps16). Number on the nodes depict range of node ages for the clades represented as the 95% HPD (Low to High) = Highest Posterior Density. Each species in the Hawaiian clade is color-coded. The South Pacific clade, Continental Asia clade, and Palicourea clade (outgroup) are collapsed.

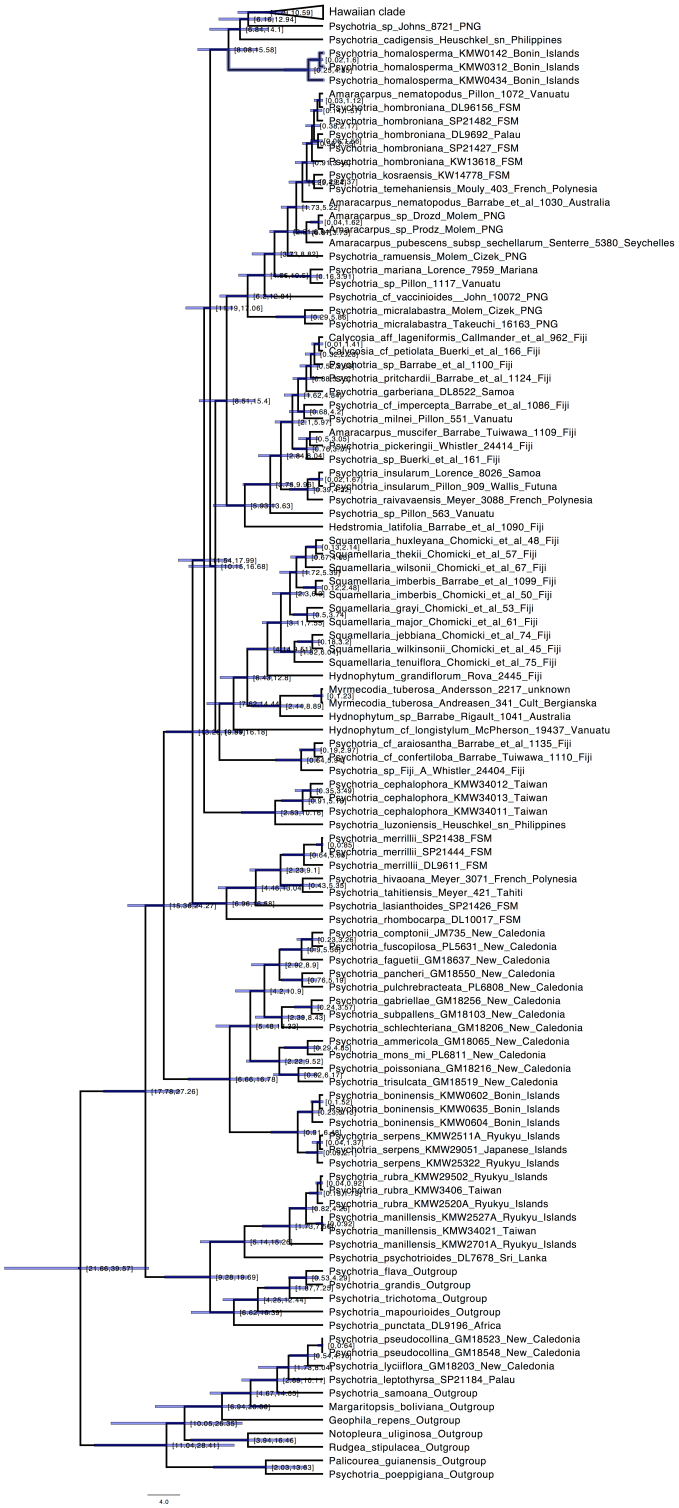


Figure 5c. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, and rps16). Number on the nodes depict range of node ages for the clades represented as the 95% HPD (Low to High) = Highest Posterior Density. The South Pacific clade, Continental Asia clade, and Palicourea clade (outgroup) are expanded and the Hawaiian clade is collapsed.

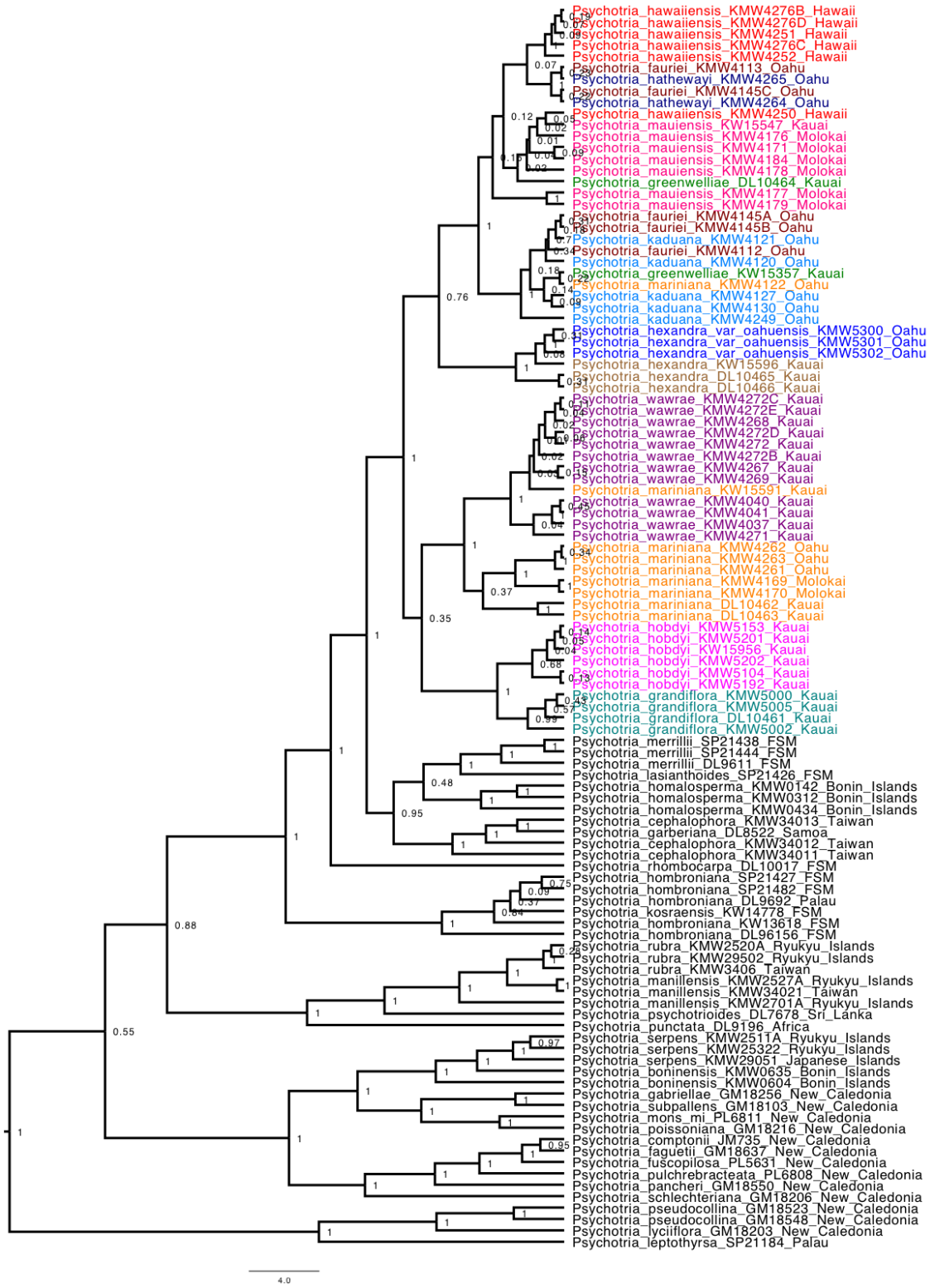


Figure 6a. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 chloroplast loci markers (psbA, psbE, rbcL, ps16, trnK, and trnT). Node numbers depict posterior probability of the clades. Species in the Hawaiian clade are color-coded.

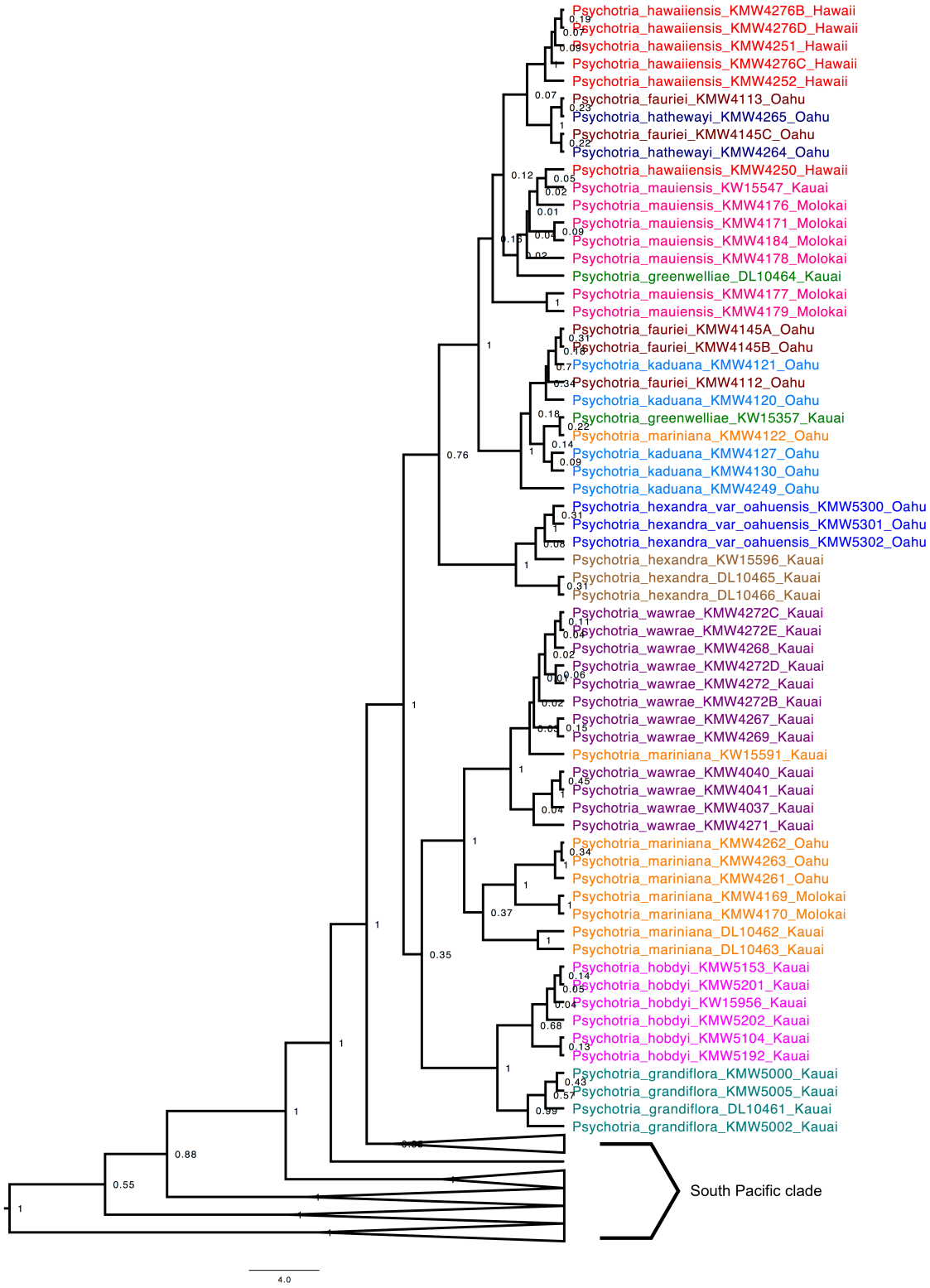


Figure 6b. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 chloroplast loci markers (psbA, psbE, rbcL, ps16, trnK, and trnT). Node numbers depict posterior probability of the clades. Each species in the Hawaiian clade is color-coded. The South Pacific clade is collapsed.

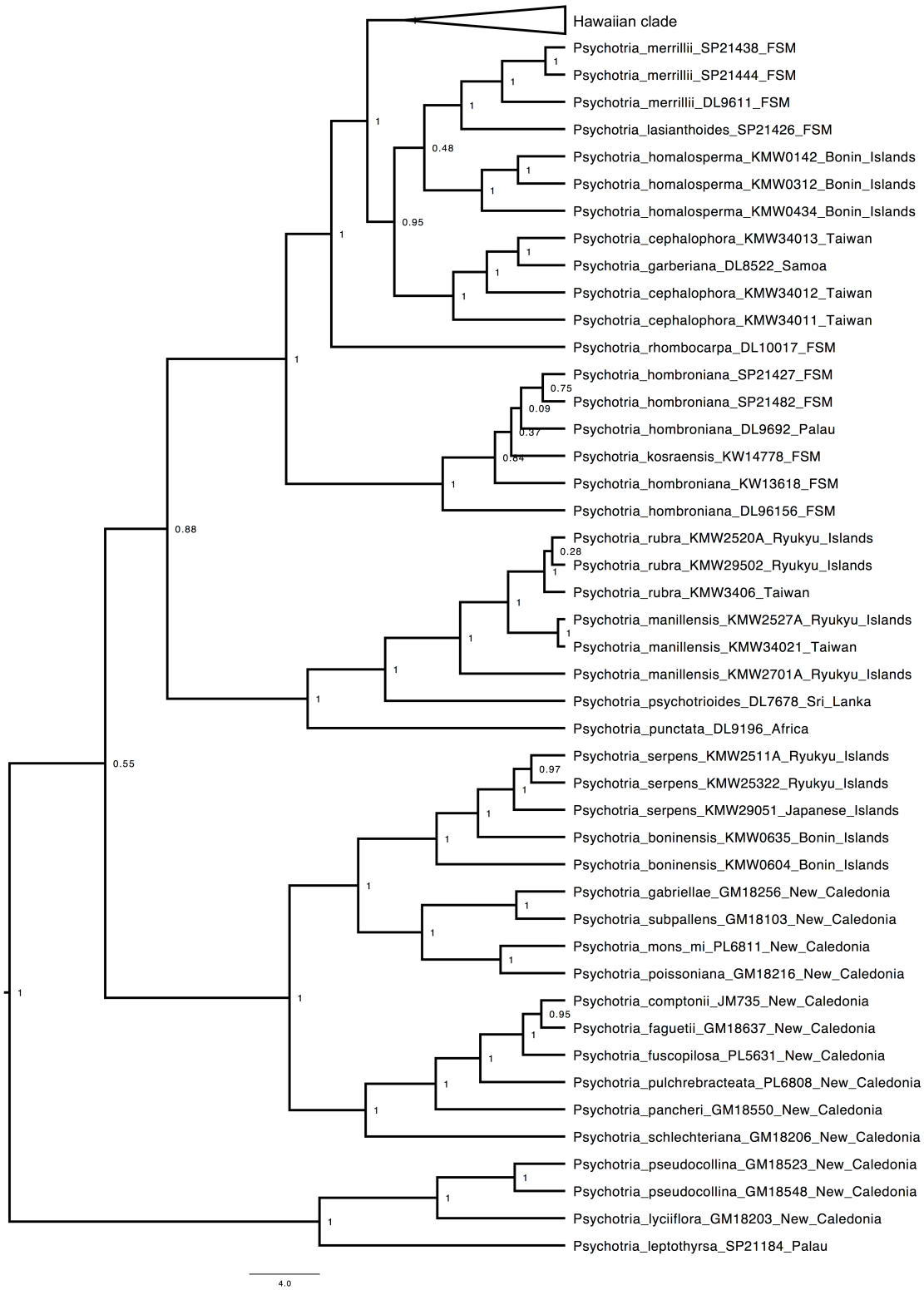


Figure 6c. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 chloroplast loci markers (psbA, psbE, rbcL, ps16, trnK, and trnT). Node numbers depict posterior probability of the clades. The South Pacific clade is expanded and the Hawaiian clade is collapsed.

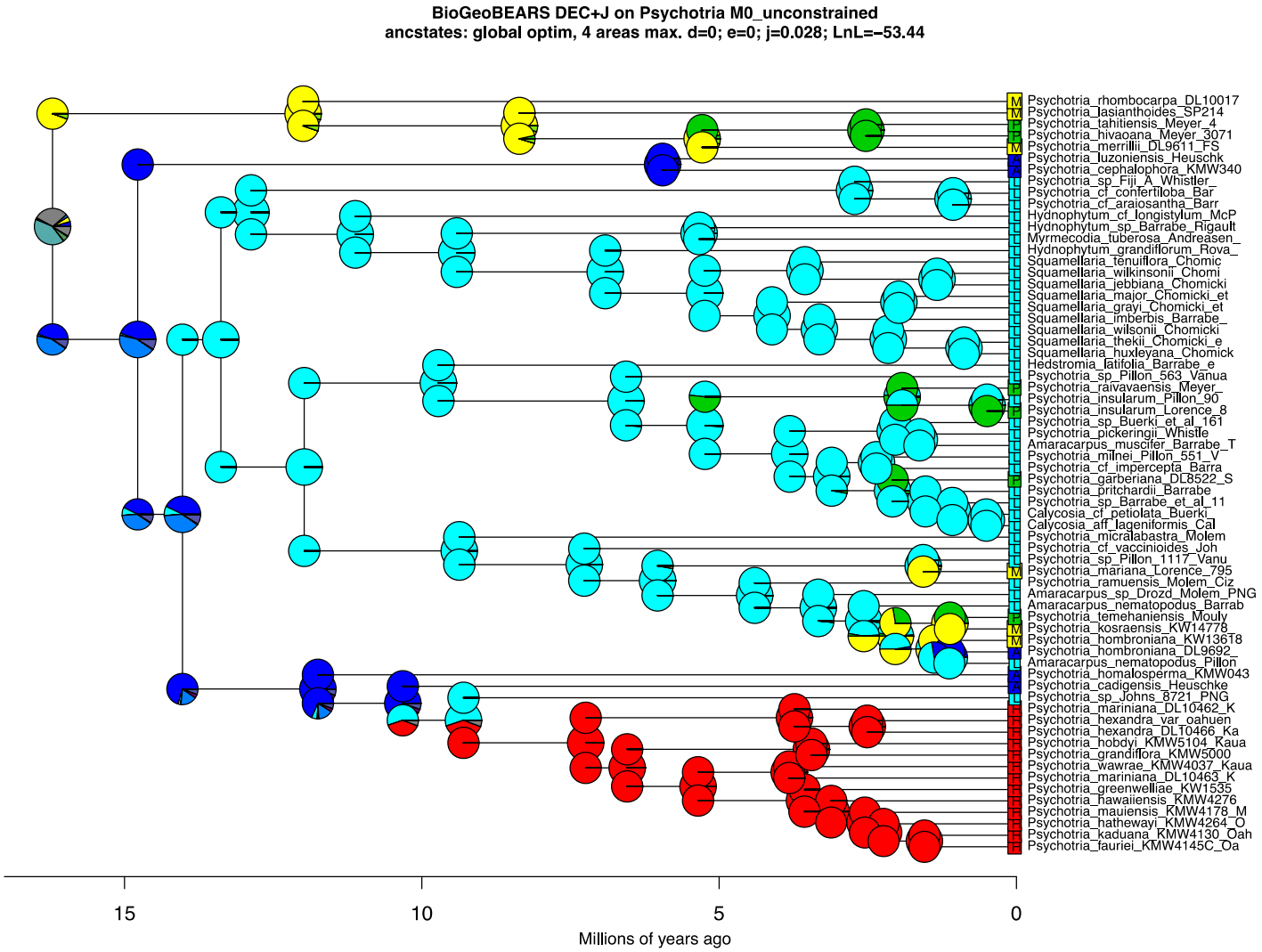


Figure 7a. Biogeographic history of Hawaiian and South Pacific *Psychotria* inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, rps16) under the DEC+J model (on the BEAST chronogram) in BioGeoBEARS analysis.

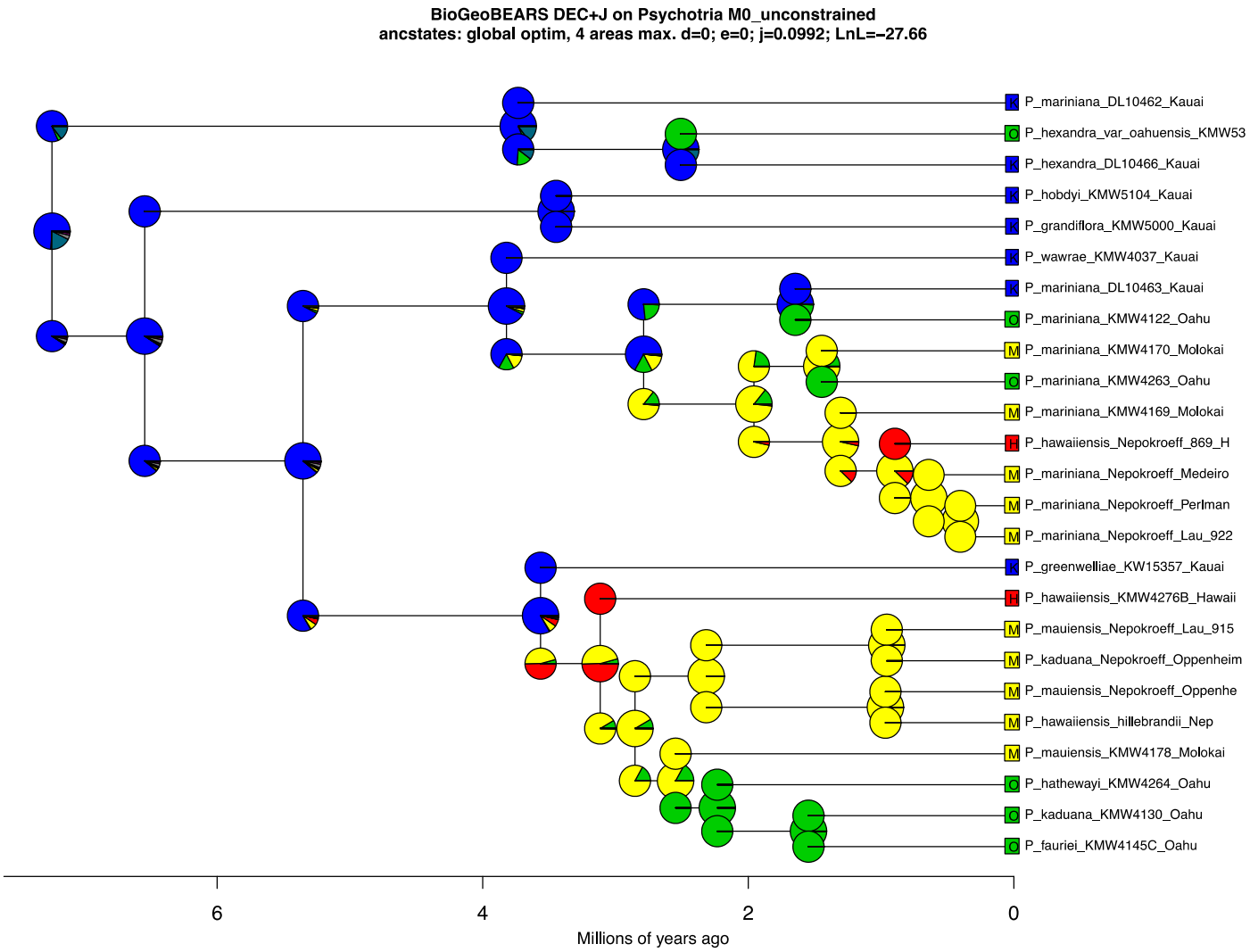


Figure 7b. Biogeographic history of Hawaiian *Psychotria* inferred using 6 loci markers (ITS, ETS, matK, psbA, rbcL, rps16) under the DEC+J model (on the BEAST chronogram) in BioGeoBEARS analysis.

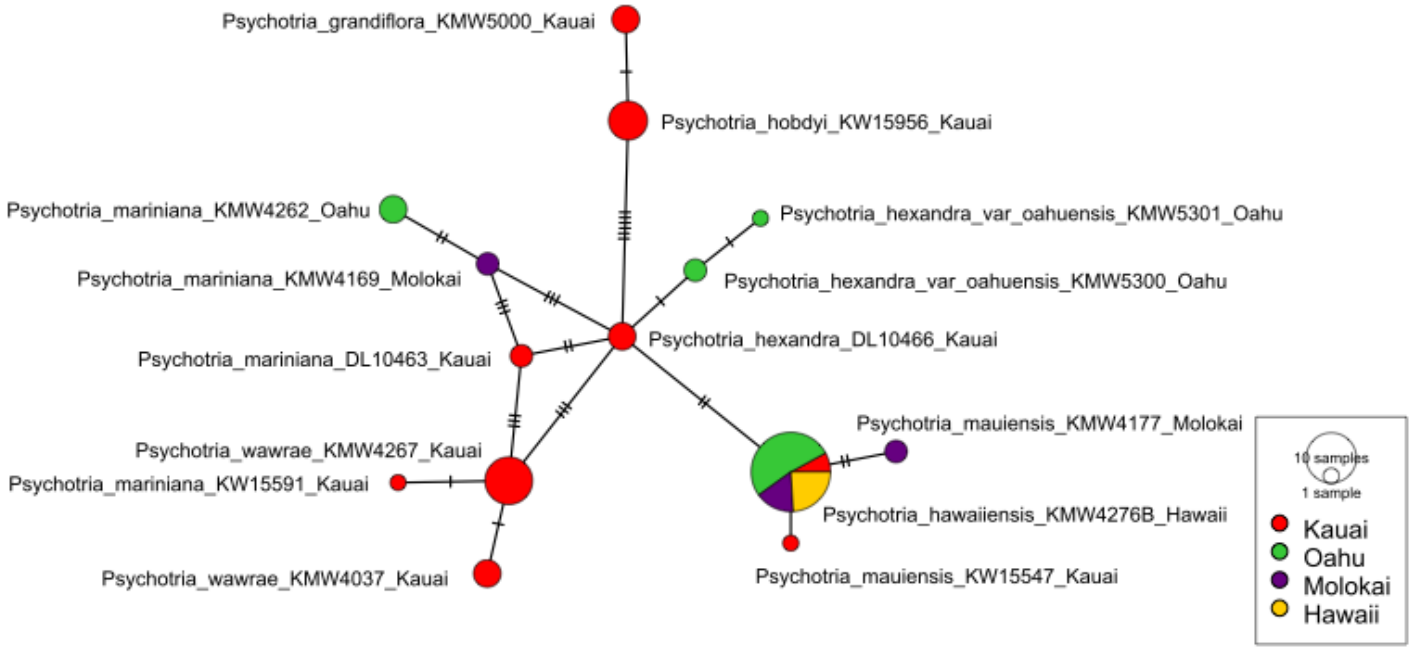


Figure 8. Haplotype network of Hawaiian *Psychotria* inferred using 6 chloroplast loci markers (psbA, psbE, rbcL, rps16, tnK, and trnT). A circle represents a haplotype sequence. Each individual color represents one of the four Hawaiian Islands: Kauai, Oahu, Molokai, and Hawaii. The number of individuals that share the same haplotype is relative to the size of the circle and the hatch marks connecting between haplotypes represent the number of mutational steps.

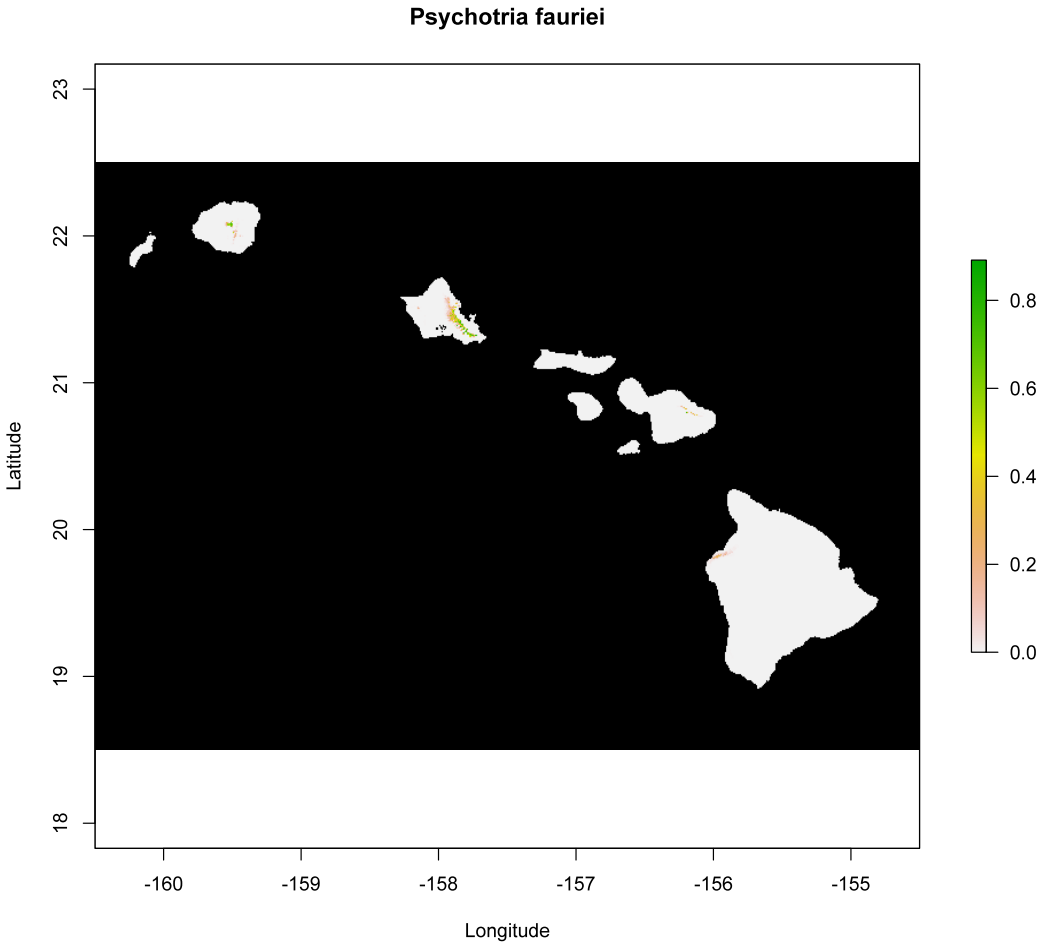


Figure 9a. Climatic niche model of *P. fauriei*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

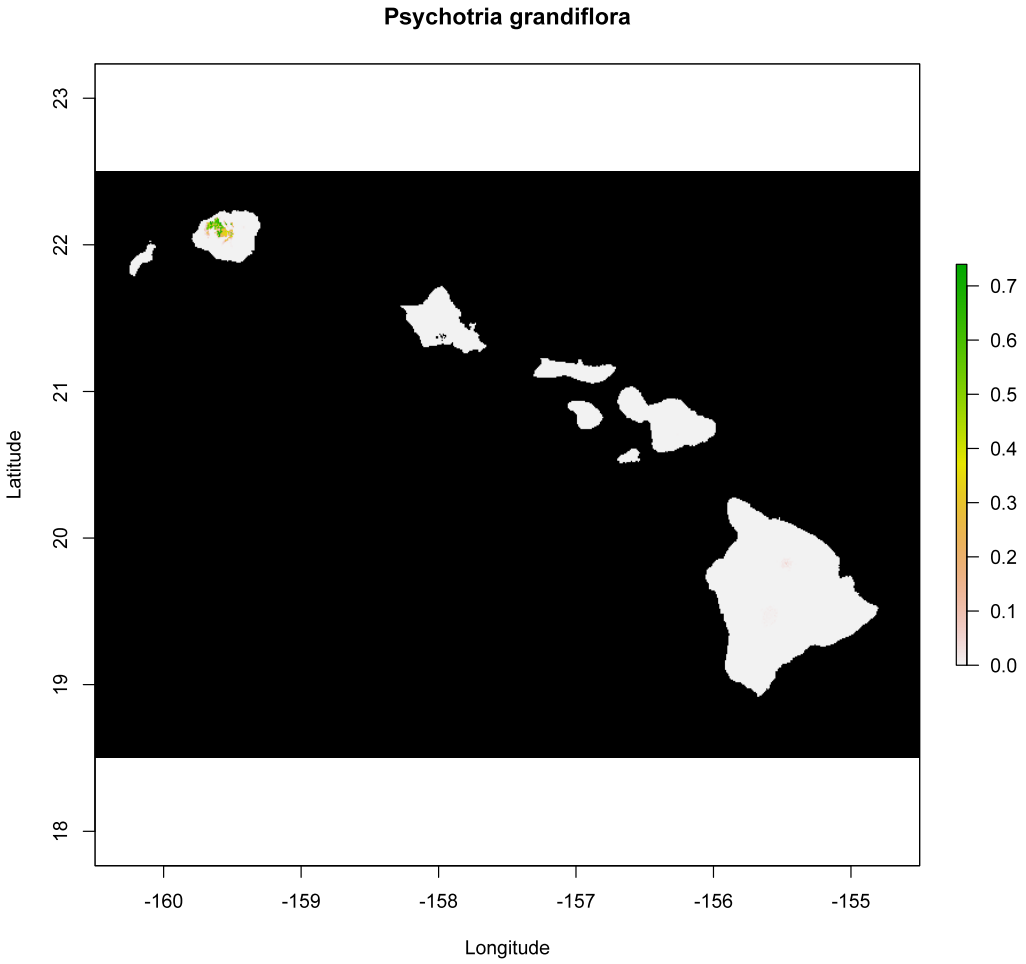


Figure 9b. Climatic niche model of *P. grandiflora*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

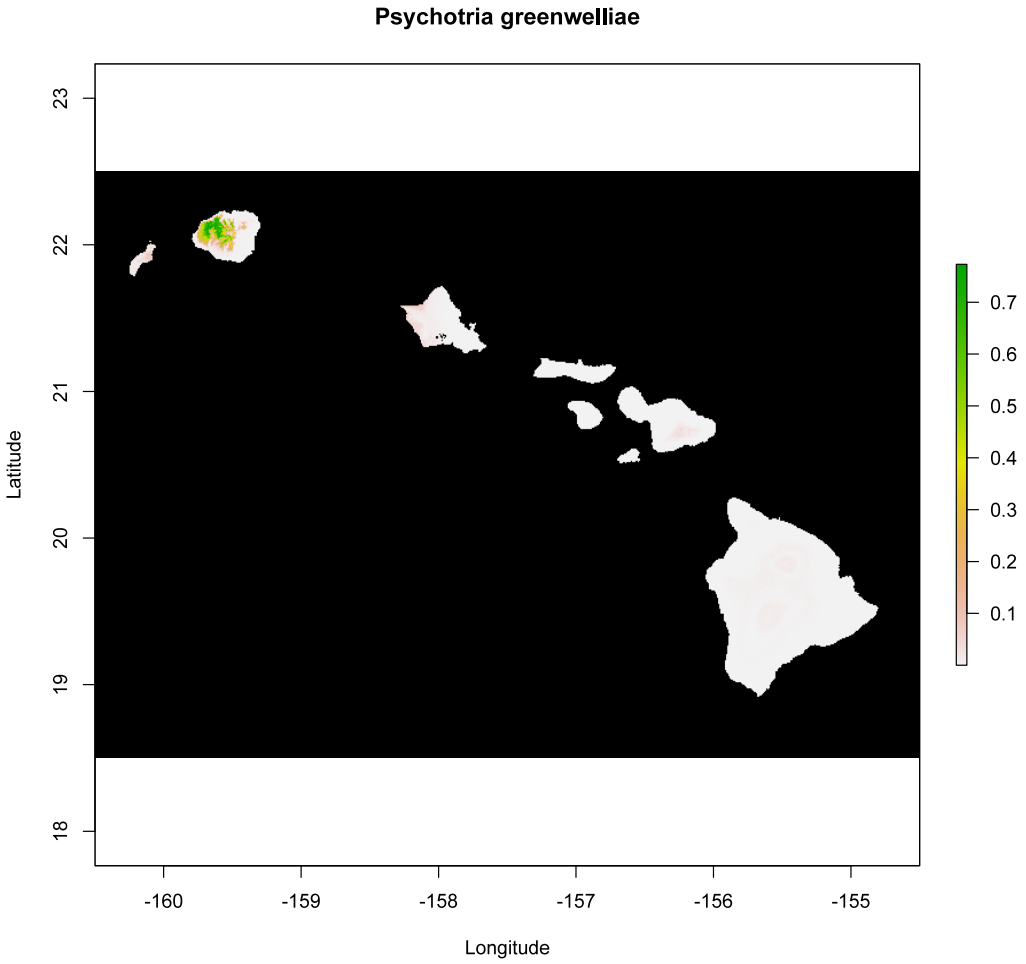


Figure 9c. Climatic niche model of *P. greenwelliae*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

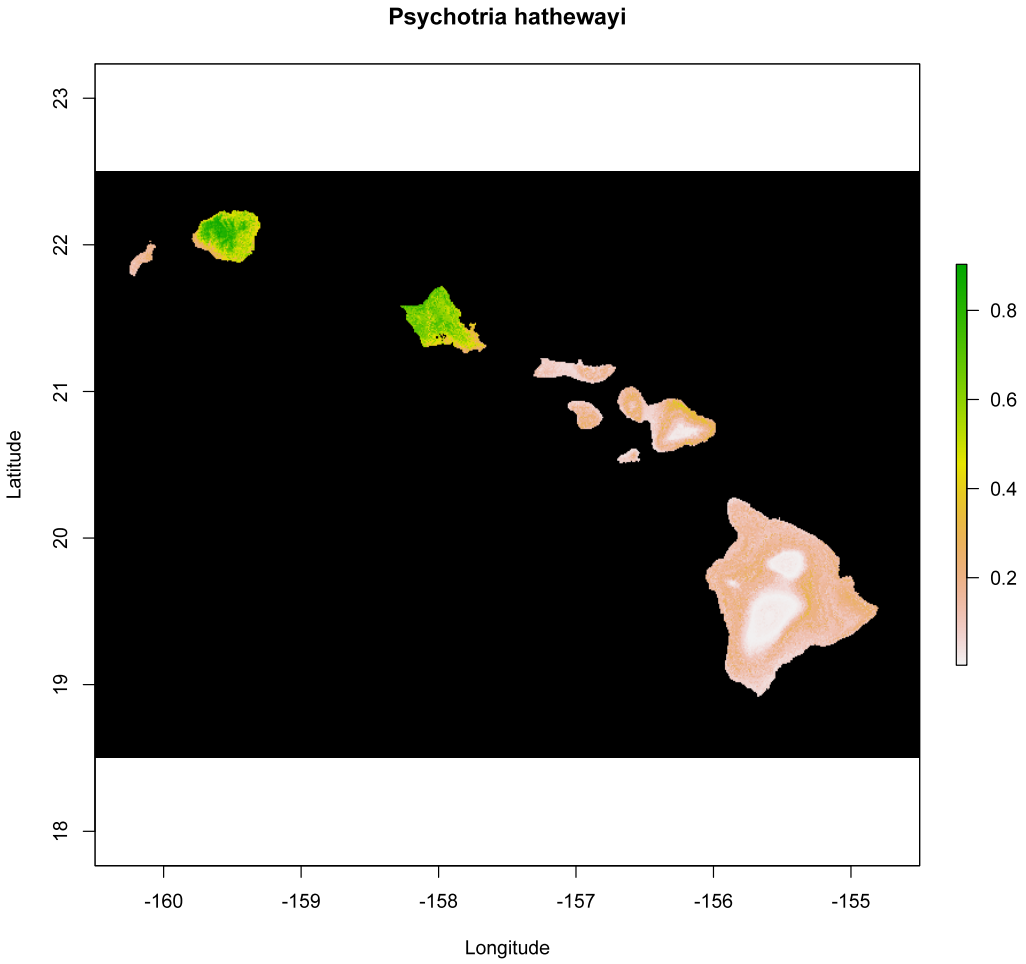


Figure 9d. Climatic niche model of *P. hathewayi*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

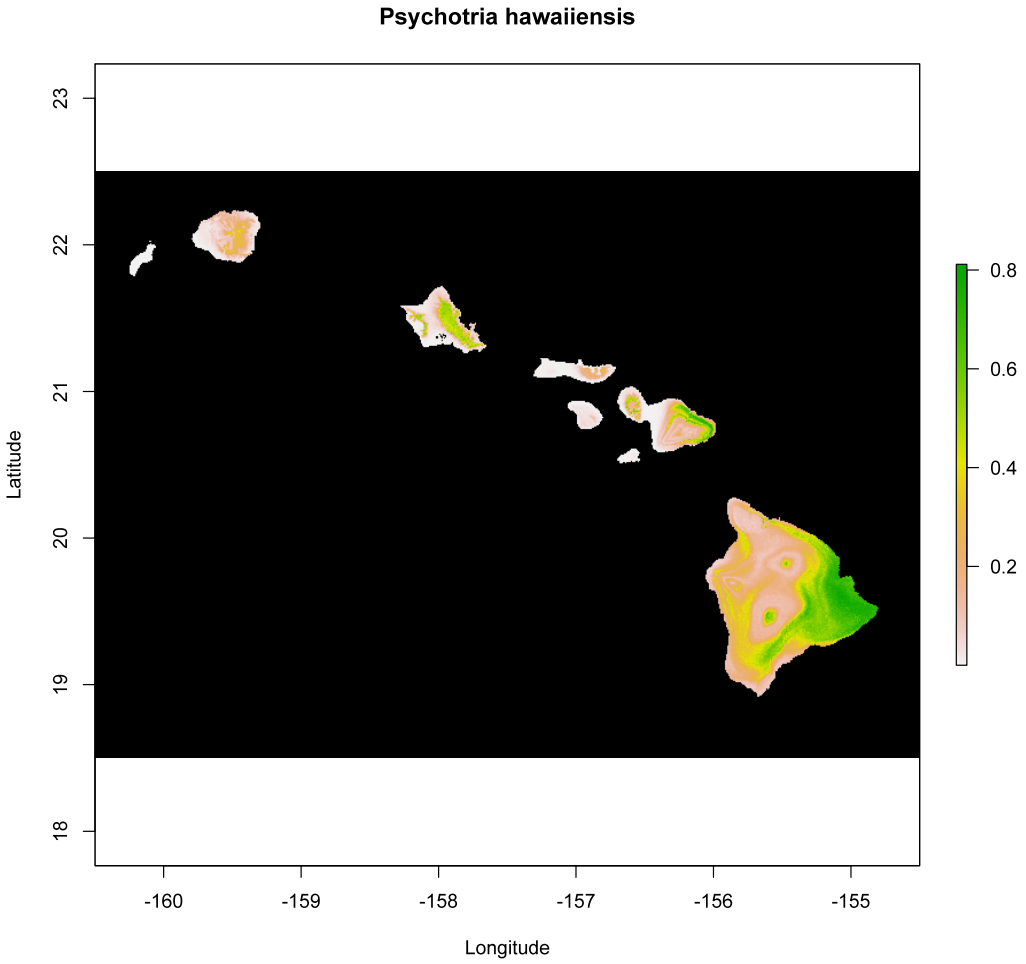


Figure 9e. Climatic niche model of *P. hawaiiensis*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

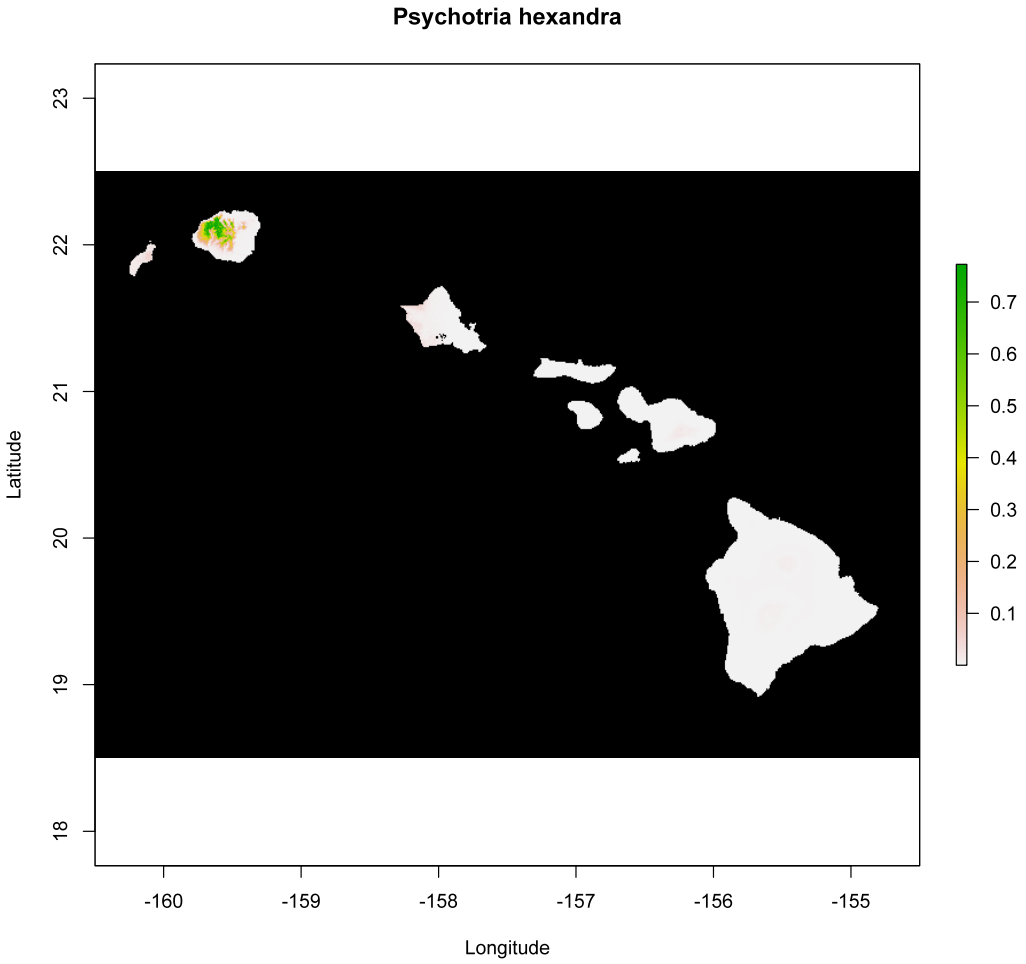


Figure 9f. Climatic niche model of *P. hexandra*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

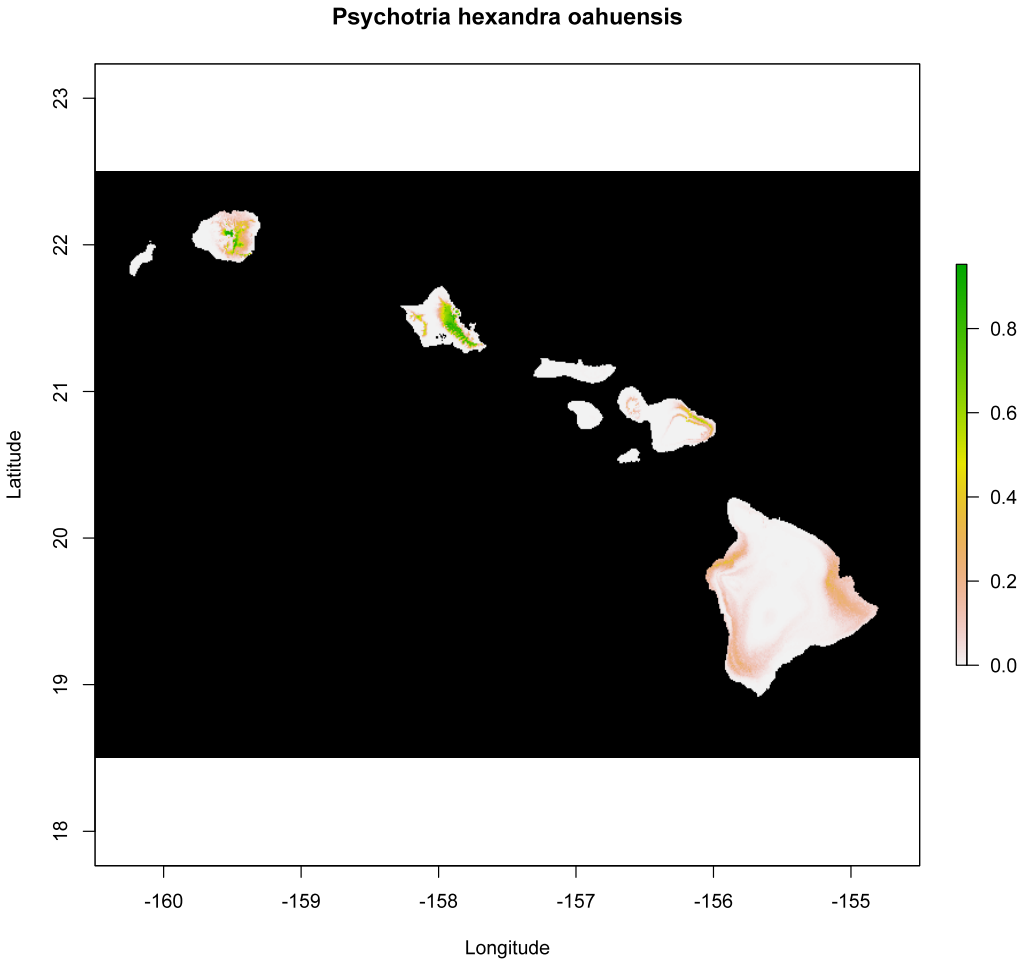


Figure 9g. Climatic niche model of *P. hexandra var. oahuensis*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

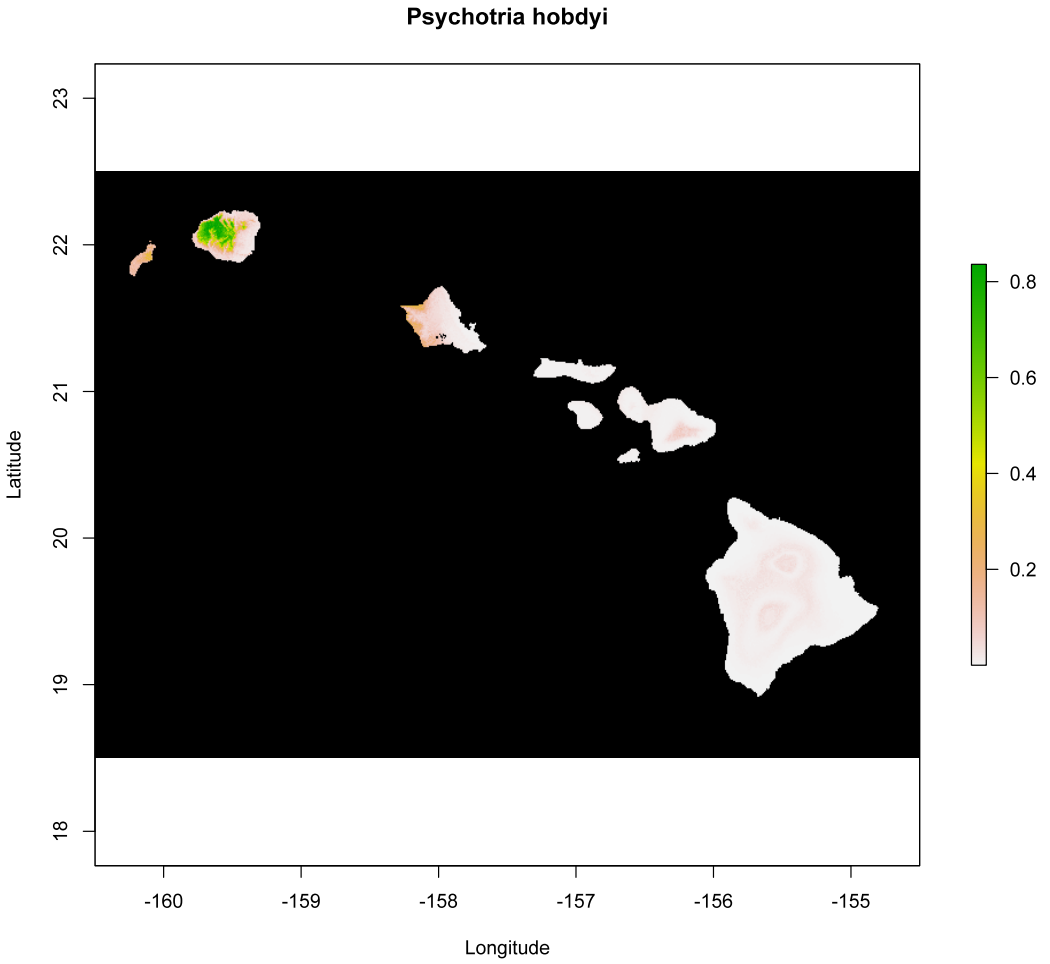


Figure 9h. Climatic niche model of *P. hobdyi*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

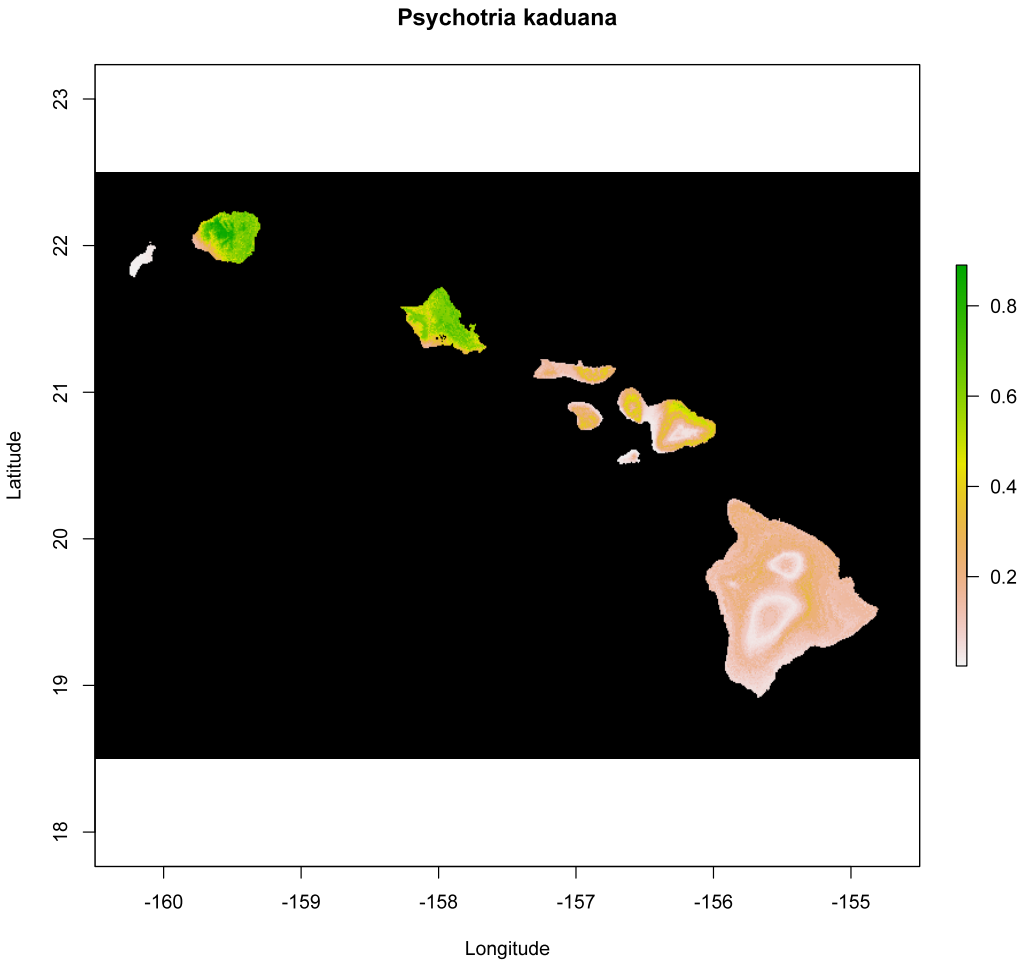


Figure 9i. Climatic niche model of *P. kaduana*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

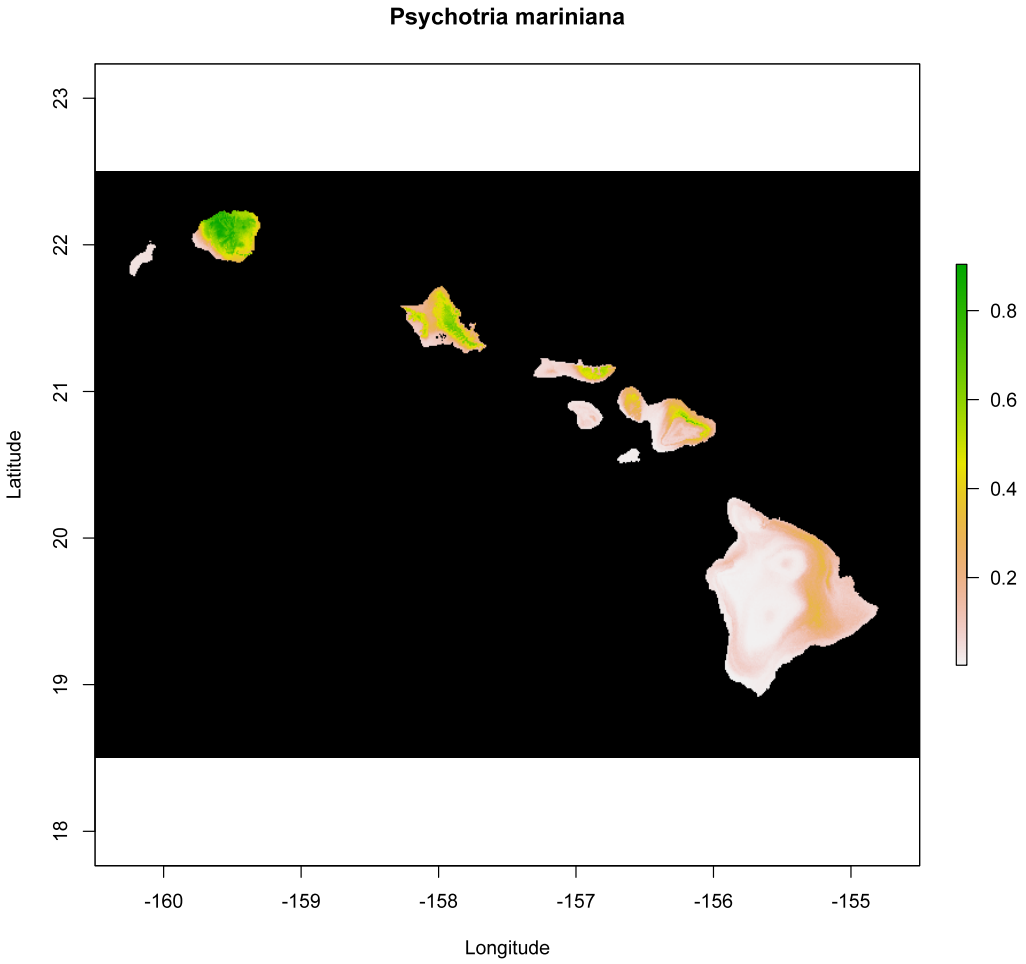


Figure 9j. Climatic niche model of *P. mariniana*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

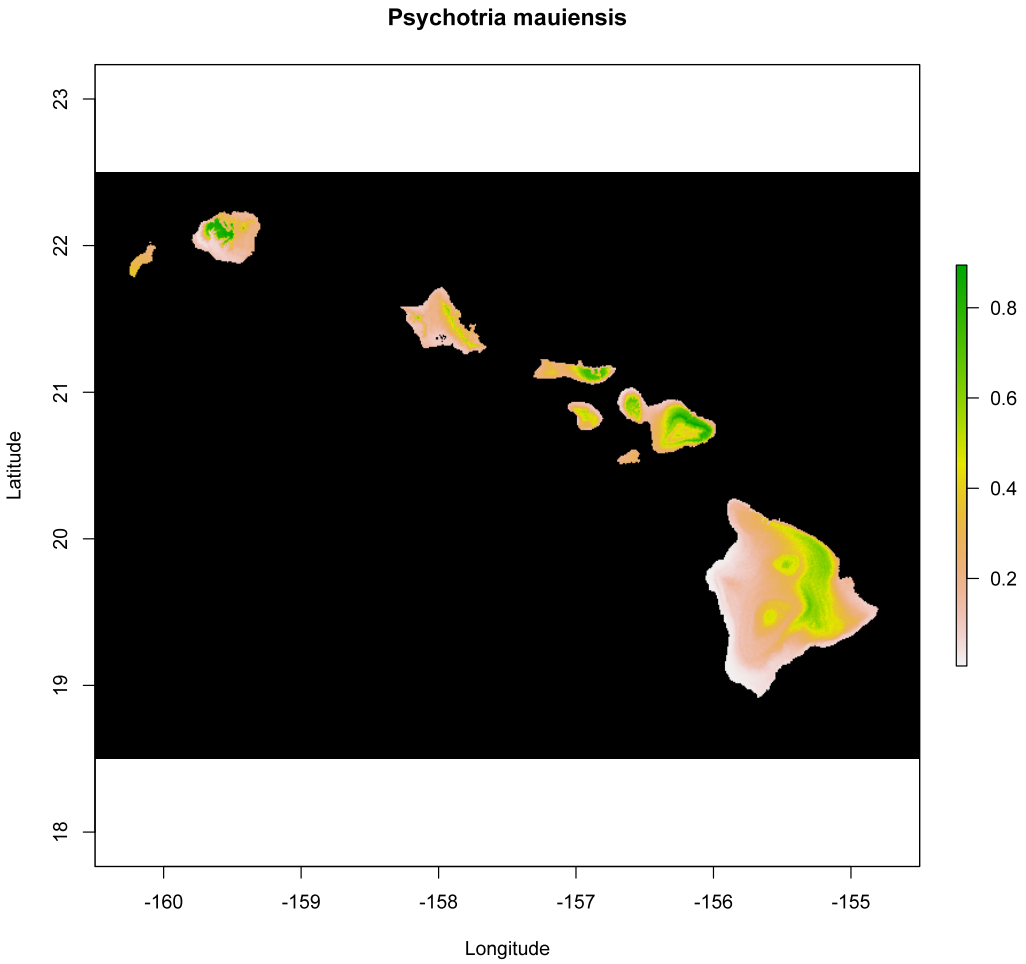


Figure 9k. Climatic niche model of *P. mauiensis*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

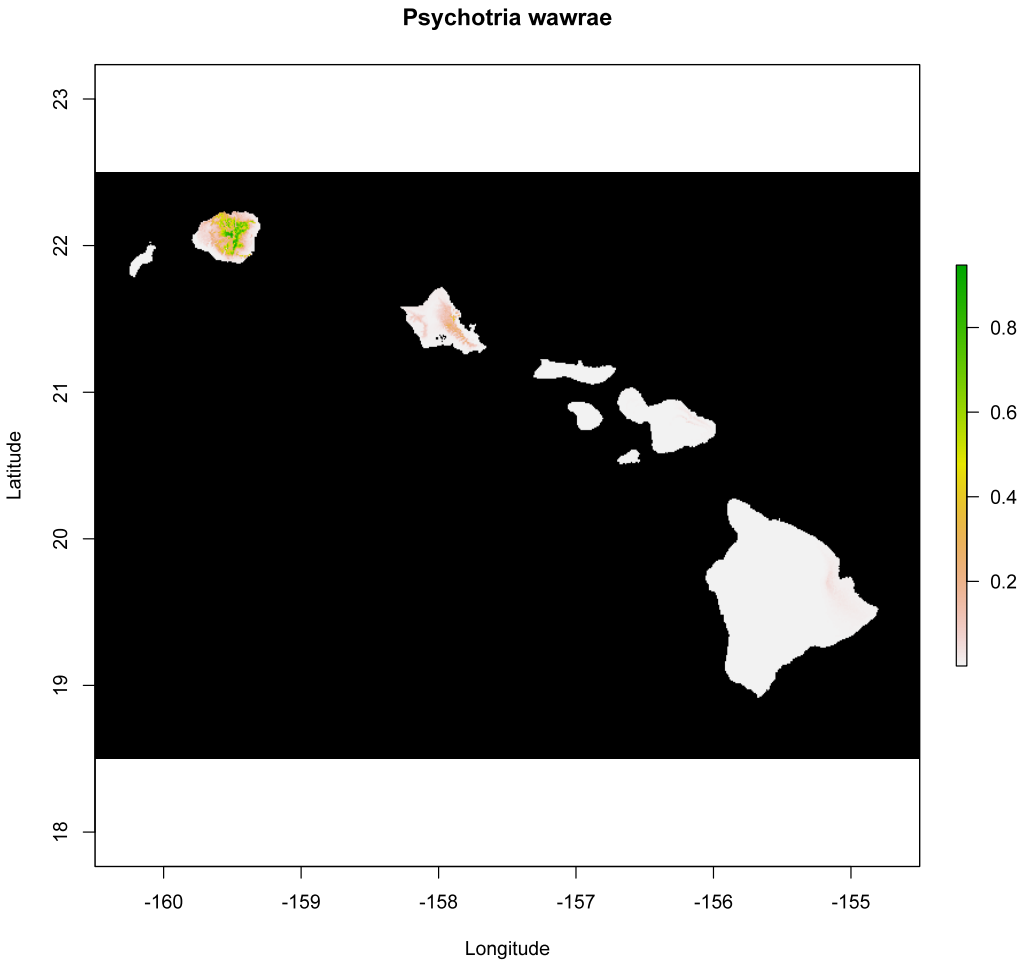


Figure 9l. Climatic niche model of *P. wawrae*, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

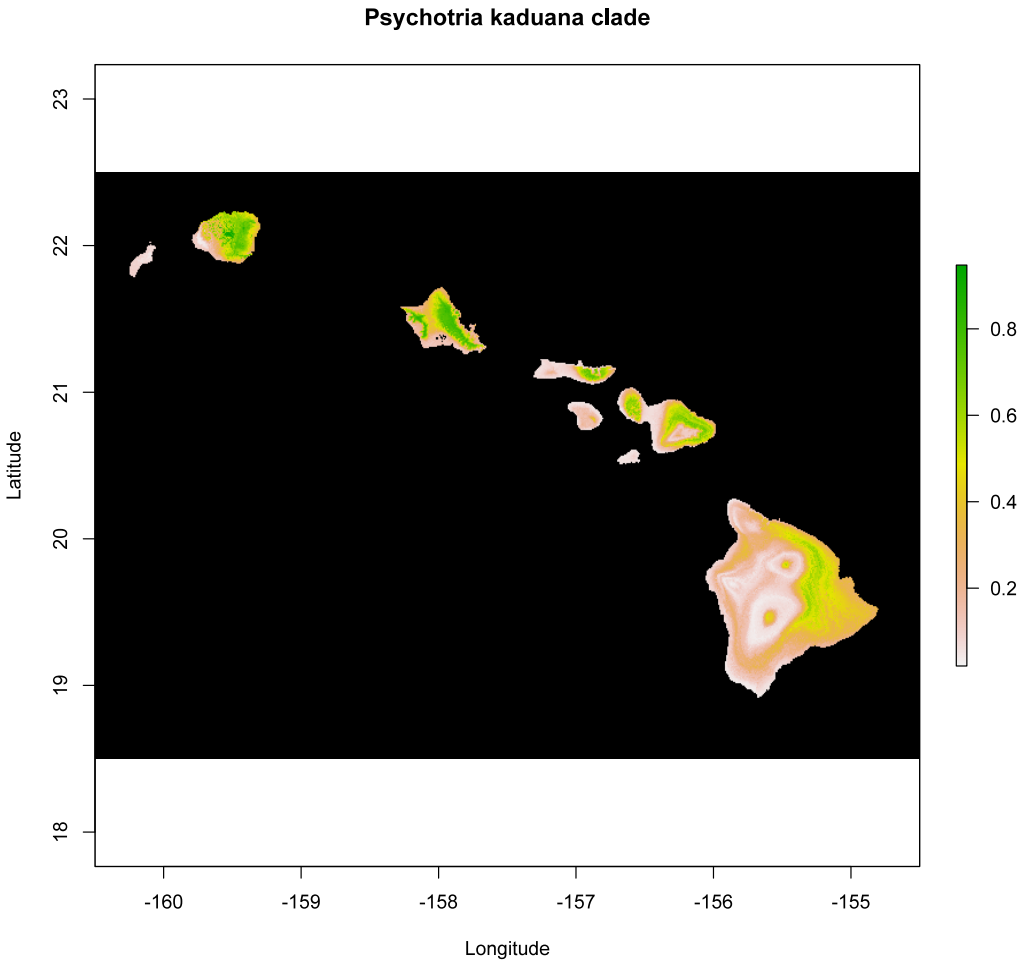


Figure 9m. Climatic niche model of *P. kaduana* clade, inferred from MaxEnt analysis. The scale represents suitability index on a scale of 0-1, with color pink/orange = less suitable, habitable areas, and color green = more suitable, habitable areas.

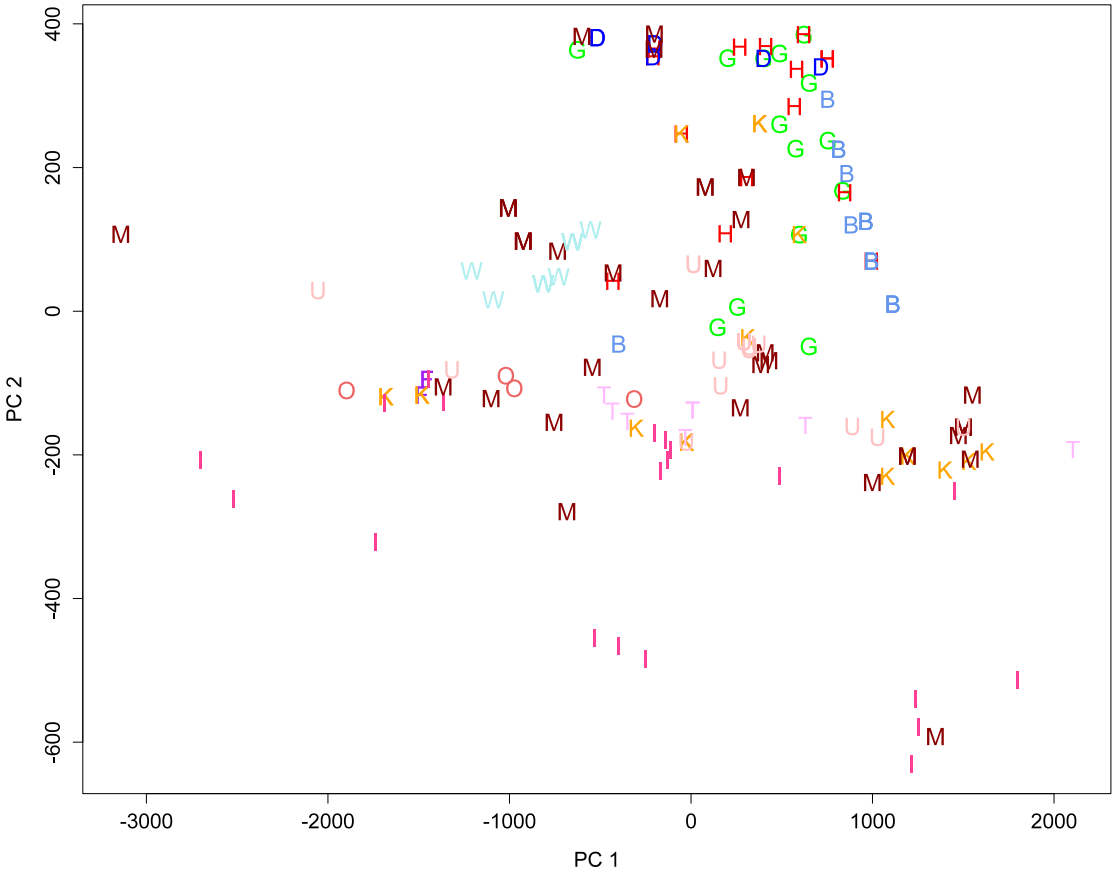


Figure 10a. Plot of the first two PCs of 19 bioclimatic variables across the Hawaiian *Psychotria* species. Individuals are labeled by letters representing their species and color coded to better visually differentiate the species. B = *P. hobdyi*, D = *P. grandiflora*, F = *P. fauriei*, G = *P. greenwelliae*, H = *P. hexandra*, I = *P. hawaiiensis*, K = *P. kaduana*, M = *P. mariniana*, O = *P. hexandra oahuensis*, T = *P. hathewayi*, U = *P. mauiensis*, W = P. *wawrae.*

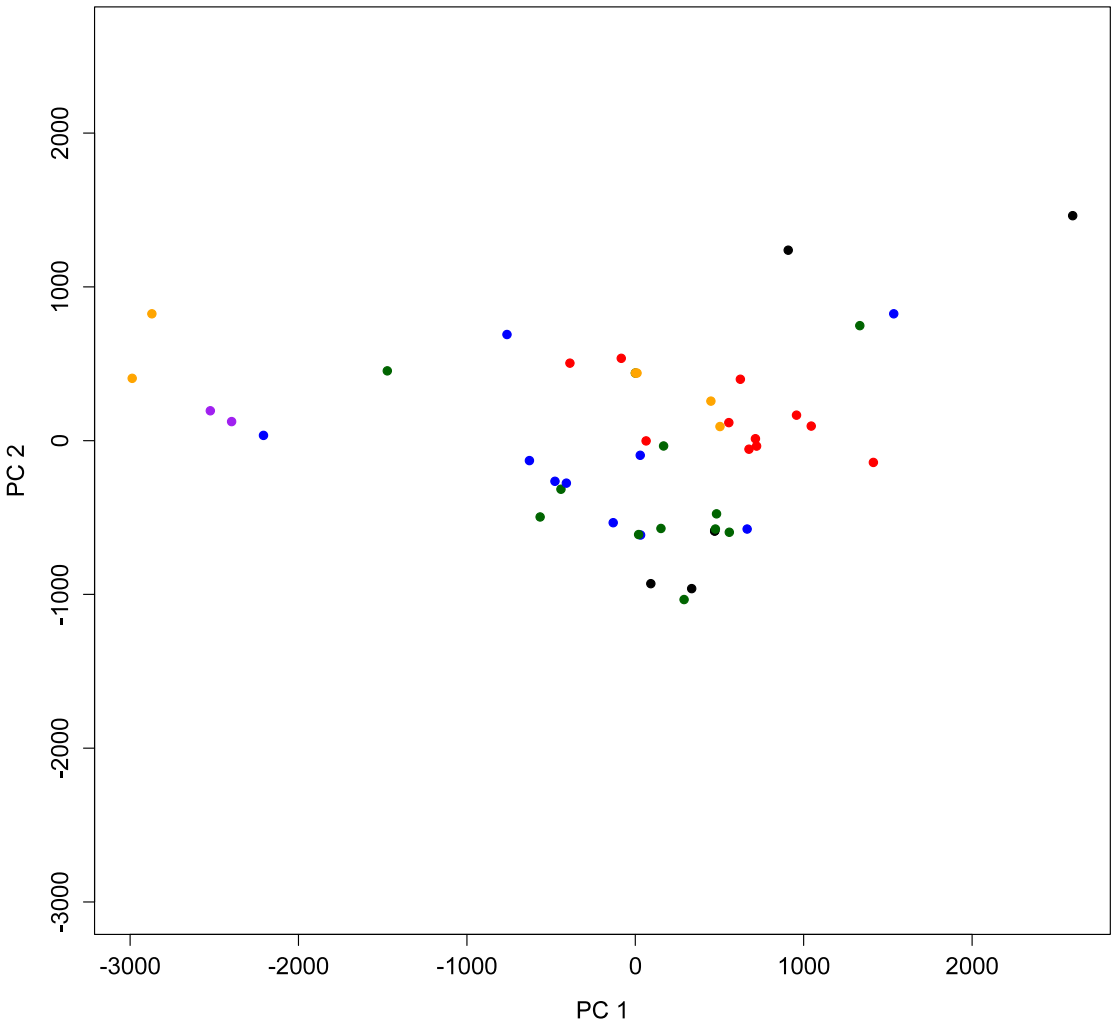
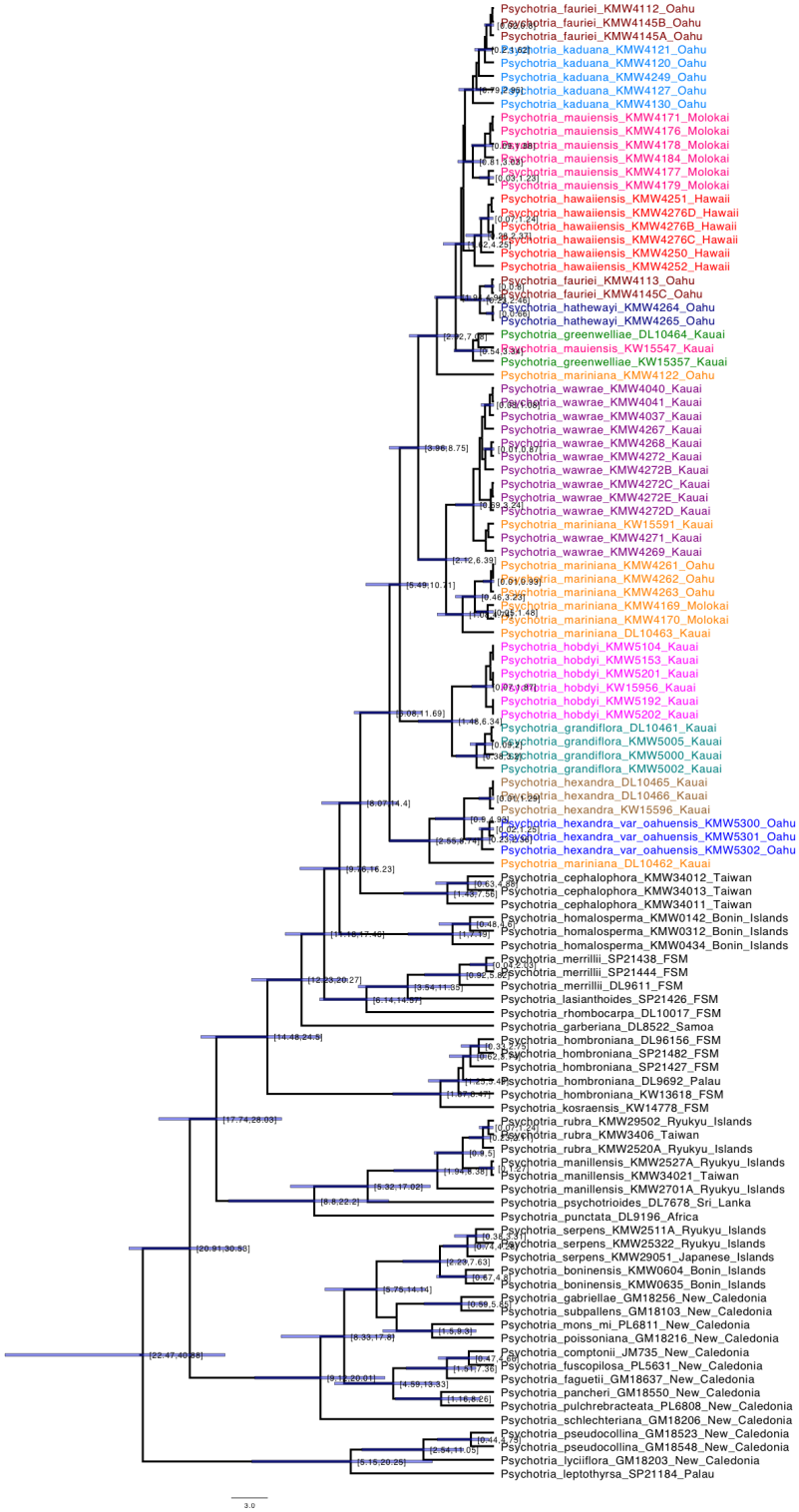
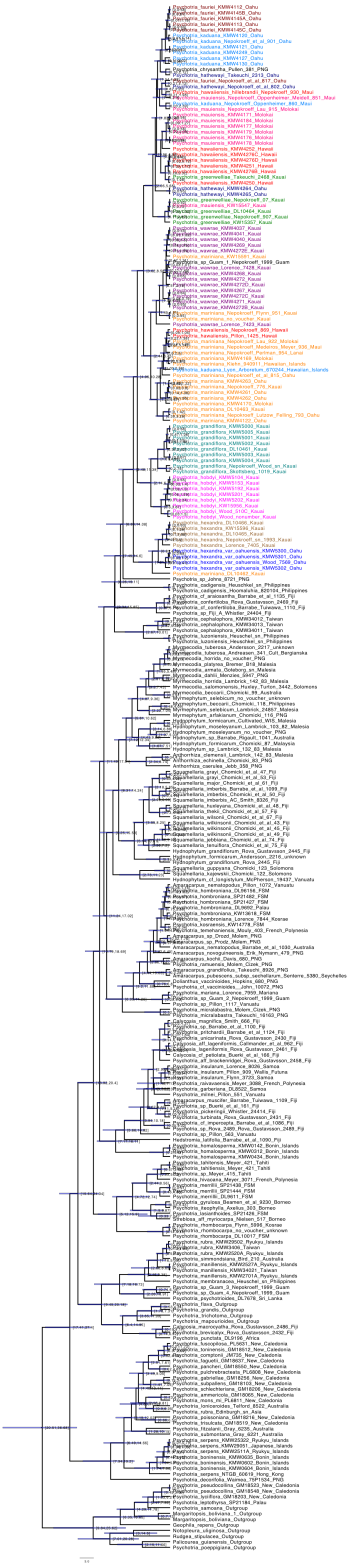


Figure 10b. Plot of the first two PCs of 19 bioclimatic variables across 36 South Pacific and 12 Hawaiian *Psychotria* species, based on the means of each species. Species are color coded by the major, well-supported clades to which they belong. Clade names refer to a species in each clade. Purple = basal *P. merrilli* clade, Orange = *P. rhombocarpa* clade, Blue = *Amaracarpus* clade, Green = *Myrmecodia* clade, Red = Hawaiian clade, Black = basal species that don't fall into the other major clades.

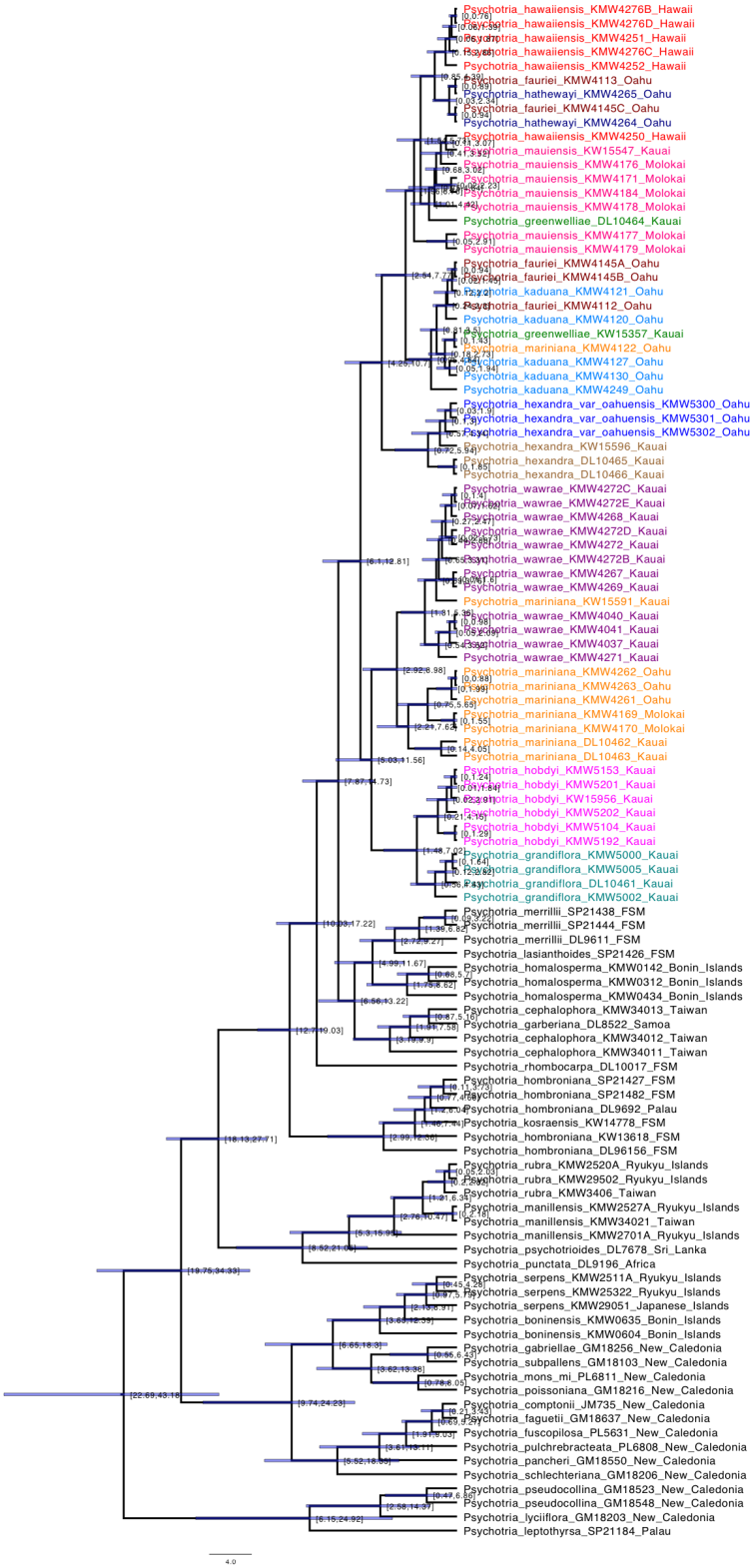
Appendices



Appendix A. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 8 loci markers (ITS, ETS, psbA, psbE, rbcL, rps16, trnK, trnT). Numbers on the nodes depict range of node ages for the clades represented as the 95% HPD (Low to High) = Highest Posterior Density. Each species in the Hawaiian clade is color-coded.



Appendix B. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 3 loci markers (ITS, ETS, and rps16). Numbers on the nodes depict range of node ages for the clades represented as the 95% HPD (Low to High) = Highest Posterior Density. Each species in the Hawaiian clade is color-coded.



Appendix C. Bayesian phylogeny of Hawaiian and South Pacific *Psychotria* species inferred using 6 loci markers (psbA, psbE, rbcL, rps16, trnK, and trnT). Numbers on the nodes depict range of node ages for the clades represented as the 95% HPD (Low to High) = Highest Posterior Density. Each species in the Hawaiian clade is color-coded.

Appendix D. Occurrence data of South Pacific *Psychotria* species. Data obtained from the Global Biodiversity Information Facility (GBIF) database, accessed on 9/1/16; as well as the NTBG, and Dr. Kenta Watanable.

Species	Latitude	Longitude
Amaracarpus_grandifolius	-6.01667	147.18333
Amaracarpus_grandifolius	-6.47877	145.24122
Amaracarpus_grandifolius	-6.5167	142.3667
Amaracarpus_grandifolius	-6.5667	146.9833
Amaracarpus_grandifolius	-6.58	142.83
Amaracarpus_grandifolius	-6.5833	142.8333
Amaracarpus_grandifolius	-6.59167	146.925
Amaracarpus_grandifolius	-7.0272	144.9303
Amaracarpus_grandifolius	-7.3	146.2333
Amaracarpus_grandifolius	-9.16667	147
Amaracarpus_grandifolius	-9.55	150.6167
Amaracarpus_grandifolius	-9.8333	150.9167
Amaracarpus_kochii	-1.15	132.48333
Amaracarpus_kochii	-2.93333	141.28333
Amaracarpus_kochii	-4.28333	137
Amaracarpus_kochii	-4.36667	136.93333
Amaracarpus_kochii	-4.38333	136.86667
Amaracarpus_kochii	-4.4	136.86667
Amaracarpus_nematopodus	-2.93333	141.28333
Amaracarpus_nematopodus	-3	141.25
Amaracarpus_nematopodus	-5.9335	146.561
Amaracarpus_nematopodus	-7.735	146.496
Amaracarpus_nematopodus	-8.58333	147.16667
Amaracarpus_nematopodus	-15.7	145.2833
Amaracarpus_nematopodus	-15.74792001	145.285
Amaracarpus_nematopodus	-15.74847001	145.2511
Amaracarpus_nematopodus	-15.7494	145.2839
Amaracarpus_nematopodus	-15.75	145.2667
Amaracarpus_nematopodus	-15.75125001	145.28999
Amaracarpus_nematopodus	-15.75680001	145.27609
Amaracarpus_nematopodus	-15.7667	145.2833
Amaracarpus_nematopodus	-15.7833	145.2667
Amaracarpus_nematopodus	-15.80681001	145.3094
Amaracarpus_nematopodus	-15.8167	145.35
Amaracarpus_nematopodus	-15.82347001	145.35941
Amaracarpus_nematopodus	-15.89014001	145.2261
Amaracarpus_nematopodus	-16.1	145.45
Amaracarpus_nematopodus	-16.16667	145.33333
Amaracarpus_nematopodus	-16.1667	145.35
Amaracarpus_nematopodus	-16.1667	145.3333
Amaracarpus_nematopodus	-16.25	145
Amaracarpus_nematopodus	-16.41514001	145.4178
Amaracarpus_nematopodus	-16.41667	145.25
Amaracarpus_nematopodus	-16.4333	145.2
Amaracarpus_nematopodus	-16.45	145.2833
Amaracarpus_nematopodus	-16.45	145.2667

Amaracarpus_nematopodus	-16.45680001	145.3761
Amaracarpus_nematopodus	-16.55	145.333
Amaracarpus_nematopodus	-16.55680001	145.3428
Amaracarpus_nematopodus	-16.5667	145.2667
Amaracarpus_nematopodus	-16.57347001	145.3261
Amaracarpus_nematopodus	-16.5833	145.2833
Amaracarpus_nematopodus	-16.9167	145.5333
Amaracarpus_nematopodus	-17.03333	145.63333
Amaracarpus_nematopodus	-17.06518001	145.60107
Amaracarpus_nematopodus	-17.08180001	145.5844
Amaracarpus_nematopodus	-17.0833	145.5667
Amaracarpus_nematopodus	-17.0833	145.5833
Amaracarpus_nematopodus	-17.1	145.6167
Amaracarpus_nematopodus	-17.10889	145.60278
Amaracarpus_nematopodus	-17.10889	145.60278
Amaracarpus_nematopodus	-17.1089	145.603
Amaracarpus_nematopodus	-17.10890001	145.6028
Amaracarpus_nematopodus	-17.1167	145.5833
Amaracarpus_nematopodus	-17.15	145.6333
Amaracarpus_nematopodus	-17.1667	145.6667
Amaracarpus_nematopodus	-17.1667	145.5833
Amaracarpus_nematopodus	-17.18419001	145.66071
Amaracarpus_nematopodus	-17.24859642	145.8508426
Amaracarpus_nematopodus	-17.25	145.85
Amaracarpus_nematopodus	-17.25	145.83333
Amaracarpus_nematopodus	-17.25	145.85
Amaracarpus_nematopodus	-17.2667	145.85
Amaracarpus_nematopodus	-17.2667	145.4
Amaracarpus_nematopodus	-17.2667	145.85
Amaracarpus_nematopodus	-17.26786001	145.6732
Amaracarpus_nematopodus	-17.2833	145.45
Amaracarpus_nematopodus	-17.2833	145.5667
Amaracarpus_nematopodus	-17.2833	145.8833
Amaracarpus_nematopodus	-17.28333	145.45
Amaracarpus_nematopodus	-17.30663001	145.8009
Amaracarpus_nematopodus	-17.31667	145.43333
Amaracarpus_nematopodus	-17.3333	145.8333
Amaracarpus_nematopodus	-17.3333	145.4167
Amaracarpus_nematopodus	-17.33333	145.41667
Amaracarpus_nematopodus	-17.35168001	145.778
Amaracarpus_nematopodus	-17.35621001	145.78081
Amaracarpus_nematopodus	-17.38192599	145.8008436
Amaracarpus_nematopodus	-17.3833	145.8
Amaracarpus_nematopodus	-17.38333	145.38333
Amaracarpus_nematopodus	-17.41513001	145.9178
Amaracarpus_nematopodus	-17.41513001	145.5844
Amaracarpus_nematopodus	-17.4167	145.4833
Amaracarpus_nematopodus	-17.4267	145.4861
Amaracarpus_nematopodus	-17.44947001	145.8094
Amaracarpus_nematopodus	-17.4667	145.5
Amaracarpus_nematopodus	-17.49972001	145.6805

Amaracarpus_nematopodus	-17.5167	145.8333
Amaracarpus_nematopodus	-17.55	145.55
Amaracarpus_nematopodus	-17.60707001	145.778
Amaracarpus_nematopodus	-17.75	145.7
Amaracarpus_nematopodus	-17.83	145.53
Amaracarpus_nematopodus	-17.8333	145.5333
Amaracarpus_nematopodus	-17.84945	145.5417
Amaracarpus_nematopodus	-17.99440001	145.8661
Amaracarpus_nematopodus	-17.99444	145.86611
Amaracarpus_nematopodus	-18.0167	145.6
Amaracarpus_nematopodus	-18.16402001	145.6978
Amaracarpus_nematopodus	-18.1656	145.6967
Amaracarpus_novoguineensis	-4	137
Amaracarpus_novoguineensis	-4.11667	137.11667
Amaracarpus_novoguineensis	-5.25	141.66667
Anthorrhiza_caerulea	-6.85	146.71667
Anthorrhiza_caerulea	-6.85833	146.725
Anthorrhiza_caerulea	-7.33333	146.66667
Anthorrhiza_caerulea	-7.51667	146.78333
Anthorrhiza_echinella	-6.9	146.61667
Anthorrhiza_echinella	-7.41667	147.16667
Anthorrhiza_echinella	-7.41667	147.25
Anthorrhiza_echinella	-7.425	147.175
Anthorrhiza_echinella	-7.425	147.25833
Calycosia_lageniformis	-17.73056	178.04917
Calycosia_lageniformis	-17.73	178.05
Dolianthus_vaccinioides	-5.83333	144.75
Dolianthus_vaccinioides	-6.71667	145.96667
Dolianthus_vaccinioides	-8.38333	147.4
Dolianthus_vaccinioides	-8.66667	147.5
Dolianthus_vaccinioides	-8.675	147.50833
Dolianthus_vaccinioides	-8.75	147.48333
Dolianthus_vaccinioides	-8.8833	147.5333
Dolianthus_vaccinioides	-8.91667	147.58333
Dolianthus_vaccinioides	-8.91667	147.5
Dolianthus_vaccinioides	-8.925	147.59167
Hydnophytum_formicarum	16.12639	107.74806
Hydnophytum_formicarum	15.66667	121.3
Hydnophytum_formicarum	14.5	104
Hydnophytum_formicarum	13.42944	103.76361
Hydnophytum_formicarum	12.12567	109.00733
Hydnophytum_formicarum	11.58972	103.07389
Hydnophytum_formicarum	9	98.16667
Hydnophytum_formicarum	6.3	124.55
Hydnophytum_formicarum	4.66667	100.83333
Hydnophytum_formicarum	4.5	115.16667
Hydnophytum_formicarum	4.33333	114.85
Hydnophytum_formicarum	2.04194	128.35028
Hydnophytum_formicarum	0.81667	127.86667
Hydnophytum_formicarum	0.75	121.5
Hydnophytum_formicarum	0.75	121.5

Hydnophytum_formicarum	0.69744	128.01836
Hydnophytum_formicarum	0.68228	127.98564
Hydnophytum_formicarum	0.56667	127.6
Hydnophytum_formicarum	0.53725	128.00211
Hydnophytum_formicarum	0.50989	128.00756
Hydnophytum_formicarum	-0.31667	127.73333
Hydnophytum_formicarum	-0.61667	112.25
Hydnophytum_formicarum	-0.75	127.53333
Hydnophytum_formicarum	-0.81667	116.46667
Hydnophytum_formicarum	-1.46667	127.5
Hydnophytum_formicarum	-1.81667	115.73333
Hydnophytum_formicarum	-2.23028	117.30056
Hydnophytum_formicarum	-3.09433	126.36696
Hydnophytum_formicarum	-3.67525	127.19028
Hydnophytum_formicarum	-3.76667	126.51667
Hydnophytum_formicarum	-3.77177	121.64853
Hydnophytum_formicarum	-4.16667	144.86667
Hydnophytum_formicarum	-4.3494	145.101
Hydnophytum_formicarum	-6.33333	142.08333
Hydnophytum_formicarum	-7.50278	111.26306
Hydnophytum_formicarum	-10.74856	142.50108
Hydnophytum_formicarum	-10.8833	142.3833
Hydnophytum_formicarum	-12.7	143.3
Hydnophytum_formicarum	-13.66667	143.41667
Hydnophytum_formicarum	-17.35	145.9167
Hydnophytum_grandiflorum	-17.73	178.05
Hydnophytum_grandiflorum	-17.73028	178.04917
Hydnophytum_moseleyanum	-2.16667	146.91667
Hydnophytum_moseleyanum	-2.16667	147
Hydnophytum_moseleyanum	-2.5	140.5
Hydnophytum_moseleyanum	-2.5	140.5
Hydnophytum_moseleyanum	-2.75	141.35
Hydnophytum_moseleyanum	-2.83333	141.58333
Hydnophytum_moseleyanum	-2.83333	141.25
Hydnophytum_moseleyanum	-2.83333	141.583
Hydnophytum_moseleyanum	-2.84167	141.59167
Hydnophytum_moseleyanum	-3.1833	151.8
Hydnophytum_moseleyanum	-3.56667	143.63333
Hydnophytum_moseleyanum	-3.58333	143.66667
Hydnophytum_moseleyanum	-3.59167	143.675
Hydnophytum_moseleyanum	-3.66667	140.25
Hydnophytum_moseleyanum	-3.7	143.2
Hydnophytum_moseleyanum	-4.0833	144.7667
Hydnophytum_moseleyanum	-4.08333	142.83333
Hydnophytum_moseleyanum	-4.08333	144.76667
Hydnophytum_moseleyanum	-4.09167	144.775
Hydnophytum_moseleyanum	-4.13333	143.1
Hydnophytum_moseleyanum	-4.16667	144.86667
Hydnophytum_moseleyanum	-4.21667	143.11667
Hydnophytum_moseleyanum	-4.38333	152.16667
Hydnophytum_moseleyanum	-4.66667	143.58333

Hydnophytum_moseleyanum	-4.675	143.59167
Hydnophytum_moseleyanum	-5	151.38333
Hydnophytum_moseleyanum	-5.03333	151.36667
Hydnophytum_moseleyanum	-5.06667	151.8
Hydnophytum_moseleyanum	-5.07	151.8
Hydnophytum_moseleyanum	-5.16667	145.41667
Hydnophytum_moseleyanum	-5.175	145.425
Hydnophytum_moseleyanum	-5.48333	147.78333
Hydnophytum_moseleyanum	-5.5	150.58333
Hydnophytum_moseleyanum	-5.63333	143.43333
Hydnophytum_moseleyanum	-5.66667	151
Hydnophytum_moseleyanum	-5.83333	145.83333
Hydnophytum_moseleyanum	-5.9	145.73333
Hydnophytum_moseleyanum	-6.08333	150.91667
Hydnophytum_moseleyanum	-6.1	151.03333
Hydnophytum_moseleyanum	-6.10833	151.04167
Hydnophytum_moseleyanum	-6.16667	150.66667
Hydnophytum_moseleyanum	-6.17	150.67
Hydnophytum_moseleyanum	-6.18333	155.53333
Hydnophytum_moseleyanum	-6.41667	149.41667
Hydnophytum_moseleyanum	-6.5	134.58333
Hydnophytum_moseleyanum	-6.58333	140.91667
Hydnophytum_moseleyanum	-6.58333	147.83333
Hydnophytum_moseleyanum	-6.66667	146.93333
Hydnophytum_moseleyanum	-6.66667	146.78333
Hydnophytum_moseleyanum	-6.675	146.59167
Hydnophytum_moseleyanum	-6.75	147
Hydnophytum_moseleyanum	-6.75833	147.00833
Hydnophytum_moseleyanum	-7.16667	146.66667
Hydnophytum_moseleyanum	-7.175	146.675
Hydnophytum_moseleyanum	-7.51667	146.78333
Hydnophytum_moseleyanum	-7.58333	141.25
Hydnophytum_moseleyanum	-8.08333	141.25
Hydnophytum_moseleyanum	-8.68333	141.83333
Hydnophytum_moseleyanum	-8.73333	141.63333
Hydnophytum_moseleyanum	-9	142.08333
Hydnophytum_moseleyanum	-9.08333	143.16667
Hydnophytum_moseleyanum	-9.198646247	142.2008698
Hydnophytum_moseleyanum	-9.200000001	142.2
Hydnophytum_moseleyanum	-9.400000001	142.7
Hydnophytum_moseleyanum	-9.5	142.7
Hydnophytum_moseleyanum	-9.58333	147.41667
Hydnophytum_moseleyanum	-10.1	142.3
Hydnophytum_moseleyanum	-10.31667	150.46667
Hydnophytum_moseleyanum	-10.375	150.25833
Hydnophytum_moseleyanum	-10.7	142.5
Hydnophytum_moseleyanum	-10.79863586	142.5008677
Hydnophytum_moseleyanum	-10.8	142.5
Hydnophytum_moseleyanum	-10.9	142.4
Hydnophytum_moseleyanum	-11.01667	142.05
Hydnophytum_moseleyanum	-11.2	142.6

Hydnophytum_moseleyanum	-11.3986324	142.4008694
Hydnophytum_moseleyanum	-11.4	142.4
Hydnophytum_moseleyanum	-11.6	142.7
Hydnophytum_moseleyanum	-11.7	142.7
Hydnophytum_moseleyanum	-11.8	142.8
Hydnophytum_moseleyanum	-11.89862894	142.9008647
Hydnophytum_moseleyanum	-11.9	143.1
Hydnophytum_moseleyanum	-11.9	142.8
Hydnophytum_moseleyanum	-11.9	142.9
Hydnophytum_moseleyanum	-12.7	143.2
Hydnophytum_moseleyanum	-12.72	143.22
Hydnophytum_moseleyanum	-12.7439	143.2858
Hydnophytum_moseleyanum	-13.5	143.5
Hydnophytum_moseleyanum	-13.7	143.4
Hydnophytum_moseleyanum	-13.8	143.3
Hydnophytum_moseleyanum	-13.8	143.5
Hydnophytum_moseleyanum	-13.8	143.4
Hydnophytum_moseleyanum	-14	143.3
Hydnophytum_moseleyanum	-14.4	143.7
Myrmecodia_beccarii	-10.79870663	142.4009268
Myrmecodia_beccarii	-11.8	142.6
Myrmecodia_beccarii	-12.7	143.2
Myrmecodia_beccarii	-13.9	143.3
Myrmecodia_beccarii	-14	143.3
Myrmecodia_beccarii	-15.40000001	145.2
Myrmecodia_beccarii	-15.5	145.2
Myrmecodia_beccarii	-15.6	145.3
Myrmecodia_beccarii	-16.20000001	145.4
Myrmecodia_beccarii	-16.60000001	145.4
Myrmecodia_beccarii	-16.8	145.7
Myrmecodia_beccarii	-16.90000001	145.9
Myrmecodia_beccarii	-16.90000001	145.8
Myrmecodia_beccarii	-17.00000001	145.8
Myrmecodia_beccarii	-17.90000001	146
Myrmecodia_beccarii	-18.10000001	145.9
Myrmecodia_beccarii	-18.20000001	146
Myrmecodia_beccarii	-18.30000001	146.1
Myrmecodia_beccarii	-18.40000001	146.1
Myrmecodia_beccarii	-18.50000001	146.2
Myrmecodia_beccarii	-18.7	146.3
Myrmecodia_horrida	-5.75	145.18333
Myrmecodia_horrida	-6	143
Myrmecodia_horrida	-5.95	143.98333
Myrmecodia_horrida	-6.2	143.95
Myrmecodia_salomonensis	-9.46667	159.96667
Myrmecodia_salomonensis	-5.01667	150.13333
Myrmecodia_salomonensis	-6.18333	155.46667
Myrmecodia_tuberosa	15.66667	121.3
Myrmecodia_tuberosa	13	122
Myrmecodia_tuberosa	12.77	124.05
Myrmecodia_tuberosa	12.43333	122.55

Myrmecodia_tuberosa	12.41667	122.56667
Myrmecodia_tuberosa	12.12567	109.00733
Myrmecodia_tuberosa	11.358	122.7292
Myrmecodia_tuberosa	5.75	116.35
Myrmecodia_tuberosa	4.5	115.13333
Myrmecodia_tuberosa	4.25	126.78333
Myrmecodia_tuberosa	4.11667	114.88333
Myrmecodia_tuberosa	3.666	115.833
Myrmecodia_tuberosa	-1.21667	120.11667
Myrmecodia_tuberosa	-1.66667	150
Myrmecodia_tuberosa	-2.36667	150.2
Myrmecodia_tuberosa	-2.3667	150.2
Myrmecodia_tuberosa	-3.11667	152.65
Myrmecodia_tuberosa	-3.2	141.35
Myrmecodia_tuberosa	-4.3	152.11667
Myrmecodia_tuberosa	-4.3	152.11667
Myrmecodia_tuberosa	-4.34788	152.241
Myrmecodia_tuberosa	-4.34788	152.241
Myrmecodia_tuberosa	-4.453	152.938
Myrmecodia_tuberosa	-4.93333	151.43333
Myrmecodia_tuberosa	-5.01667	150.13333
Myrmecodia_tuberosa	-6.16667	155.33333
Myrmecodia_tuberosa	-6.175	155.34167
Myrmecodia_tuberosa	-6.18333	155.46667
Myrmecodia_tuberosa	-6.51667	143.16667
Myrmecodia_tuberosa	-6.83333	134.33333
Myrmecodia_tuberosa	-7.35	146.68333
Myrmecodia_tuberosa	-7.36167	147.13833
Myrmecodia_tuberosa	-7.88333	146.61667
Myrmecodia_tuberosa	-8.463890001	127.16333
Myrmecodia_tuberosa	-9.46667	159.96667
Myrmecodia_tuberosa	-12.6667	143.3333
Myrmecodia_tuberosa	-12.7	143.3
Myrmecodia_tuberosa	-12.8	143.3
Myrmecodia_tuberosa	-13.7	143.4
Myrmecodia_tuberosa	-13.7	143.4
Myrmecodia_tuberosa	-13.79861794	143.4008623
Myrmecodia_tuberosa	-13.8	143.4
Myrmecodia_tuberosa	-13.9	143.5
Myrmecodia_tuberosa	-13.9	143.25
Myrmecodia_tuberosa	-14	143.3
Myrmephytum_arfakianum	-1.14164	133.89594
Myrmephytum_arfakianum	-1.41667	133.91667
Psychotria_brackenridgei	17.73028	178.04917
Psychotria_cadigensis	11.358	122.7292
Psychotria_cephalophora	22.65694	121.48889
Psychotria_cephalophora	22.08056	121.5275
Psychotria_cephalophora	22.07	121.53
Psychotria_cephalophora	22.06	121.52
Psychotria_cephalophora	22.05778	121.53389
Psychotria_cephalophora	22.05639	121.51444

Psychotria_cephalophora	22.05389	121.51194
Psychotria_cephalophora	22.05278	121.53389
Psychotria_cephalophora	22.05	121.52
Psychotria_cephalophora	22.05	121.53333
Psychotria_cephalophora	22.05	121.51667
Psychotria_cephalophora	22.04	121.52
Psychotria_cephalophora	22.0325	121.55611
Psychotria_cephalophora	22.03167	121.55194
Psychotria_cephalophora	22.03028	121.55361
Psychotria_cephalophora	22.03	121.56
Psychotria_cephalophora	22.0225	121.57306
Psychotria_cephalophora	22.02	121.57
Psychotria_cephalophora	22.01972	121.57639
Psychotria_cephalophora	22.01667	121.56667
Psychotria_cephalophora	22.00556	121.58472
Psychotria_garberiana	-14.2275	-169.4342
Psychotria_gyrulosa	6	116.68333
Psychotria_gyrulosa	5.98333	116.68333
Psychotria_gyrulosa	5.83333	116.31667
Psychotria_gyrulosa	5.98333	116.57083
Psychotria_gyrulosa	5.95	116.56667
Psychotria_gyrulosa	6.05	116.55
Psychotria_gyrulosa	5.98333	116.65
Psychotria_gyrulosa	5.65	117.2
Psychotria_gyrulosa	4.9625	118.19167
Psychotria_gyrulosa	5.51667	117.05
Psychotria_gyrulosa	5.86667	117.98333
Psychotria_gyrulosa	4.9625	118.19167
Psychotria_gyrulosa	5.98333	116.65
Psychotria_gyrulosa	6	116.61667
Psychotria_gyrulosa	6.2125	116.65417
Psychotria_gyrulosa	6.075	116.60417
Psychotria_gyrulosa	6.09167	116.54583
Psychotria_hombroniana	7.33833	134.48983
Psychotria_hombroniana	7.33833	134.34
Psychotria_hombroniana	7.3125	134.4461
Psychotria_hombroniana	7.21667	134.375
Psychotria_hombroniana	6.96722	158.25833
Psychotria_hombroniana	6.96	158.271
Psychotria_hombroniana	6.96	158.27056
Psychotria_hombroniana	6.96	158.271
Psychotria_hombroniana	6.94167	158.258
Psychotria_hombroniana	6.93056	158.28667
Psychotria_hombroniana	6.9139	158.2111
Psychotria_hombroniana	6.8979	158.2123
Psychotria_hombroniana	6.87056	158.16139
Psychotria_hombroniana	6.87056	158.161
Psychotria_hombroniana	6.86897	158.243
Psychotria_hombroniana	6.86682	158.19425
Psychotria_hombroniana	6.84837	158.2662
Psychotria_hombroniana	6.845	158.305

Psychotria_hombroniana	6.8378	158.2831
Psychotria_hombroniana	6.8333	158.3
Psychotria_hombroniana	6.8326	158.1837
Psychotria_hombroniana	6.8287	158.1752
Psychotria_hombroniana	6.8251	158.169
Psychotria_hombroniana	5.3543	162.9925
Psychotria_insularum	-13.86361	-171.77361
Psychotria_insularum	-13.84167	-171.74111
Psychotria_insularum	-19.6867	-175.019
Psychotria_insularum	-19.05	-169.867
Psychotria_insularum	-13.9833	-171.883,
Psychotria_insularum	-13.91667	-171.75,
Psychotria_insularum	-13.86667	-171.71667
Psychotria_insularum	-13.61	-172.44111
Psychotria_iteophylla	5.60833	117.08333
Psychotria_iteophylla	-8.3	115.15
Psychotria_iteophylla	6	116.53333
Psychotria_iteophylla	5.60833	117.08333
Psychotria_iteophylla	6.15	116.51667
Psychotria_iteophylla	6	116.58333
Psychotria_iteophylla	4.8625	117.6875
Psychotria_iteophylla	4.01667	114.85
Psychotria_iteophylla	6.01667	116.61667
Psychotria_iteophylla	5.98333	116.68333
Psychotria_iteophylla	5.575	116.80833
Psychotria_iteophylla	6.01667	116.5
Psychotria_iteophylla	2.58	115.73
Psychotria_lasianthoides	6.86897	158.24342
Psychotria_lasianthoides	6.8326	158.1837
Psychotria_lasianthoides	6.8979	158.2123
Psychotria_luzoniensis	11.358	122.7292
Psychotria_luzoniensis	10	118.75
Psychotria_micralabastra	-2.91667	141.33333
Psychotria_micralabastra	-2.95	151.35
Psychotria_micralabastra	-3	141.25
Psychotria_micralabastra	-5.23333	145.683
Psychotria_micralabastra	-5.5	145.5
Psychotria_micralabastra	-5.75278	150.222
Psychotria_micralabastra	-6.33333	146.75
Psychotria_micralabastra	-6.58333	146.41667
Psychotria_micralabastra	-6.66667	146.93333
Psychotria_micralabastra	-6.66667	146.75
Psychotria_micralabastra	-6.71667	146.78333
Psychotria_micralabastra	-6.75	146.75
Psychotria_micralabastra	-6.83333	146.58333
Psychotria_micralabastra	-6.85	146.8
Psychotria_micralabastra	-7.25	145.33333
Psychotria_micralabastra	-7.30219	147.134
Psychotria_micralabastra	-7.48333	147.26667
Psychotria_micralabastra	-7.5	147.25
Psychotria_micralabastra	-7.51667	147.35

Psychotria_micralabastra	-10.63333	150.63333
Psychotria_milnei	-19.5814	169.384
Psychotria_milnei	-15.36556	166.98333
Psychotria_pickeringii	-18.06167	178.46972
Psychotria_pickeringii	-17.74115	177.804
Psychotria_raivavaensis	-23.8667	-147.65
Psychotria_raivavaensis	-23.8833	-147.667
Psychotria_ramuensis	-2.9	141.26667
Psychotria_ramuensis	-5.5	145.4
Psychotria_ramuensis	-5.50833	145.40833
Psychotria_ramuensis	-6.75	147.08333
Psychotria_ramuensis	-7.91667	147.16667
Psychotria_ramuensis	-7.92	147.17
Psychotria_ramuensis	-7.925	147.175
Psychotria_ramuensis	-9.28233	148.277
Psychotria_ramuensis	-9.28756	148.272
Psychotria_rhombocarpa	5.30861	162.992
Psychotria_rhombocarpa	5.35	163.0017
Psychotria_rhombocarpa	5.32917	162.983
Psychotria_rhombocarpa	5.35	163.002
Psychotria_rhombocarpa	5.3075	162.992
Psychotria_tahitensis	-17.6313	-149.433
Psychotria_tahitensis	-17.6333	-149.35
Psychotria_tahitensis	-17.6667	-149.4
Psychotria_tahitensis	-17.6333	-149.433
Psychotria_vaccinioides	-3.45	136.97
Psychotria_vaccinioides	-4.21667	137.06667
Squamellaria_imberbi	-16.8333	-180
Squamellaria_imberbi	-18.0667	-178.417

Appendix E. Morphological Traits of Hawaiian *Psychotria*.

Species	Height (mm)	Fruit (mm)
P. fauriei	3000 - 9000	9 -11
P. grandiflora	5000	10 - 15
P. greenwelliae	5000	10 - 13
P. hathewayi	8000	12 - 18
P. hawaiiensis	12000	6 - 10
P. hexandra	6000	5 x 8 - 8 x 18 wide and long
P. hexandra var. hexandra	4000	9 - 15
P. hexandra var. oahuensis	4000	11 - 13
P. hobdyi	8000	8 - 9
P. kaduana	8000	5 - 15
P. mariniana	25000	10 -12
P. mauiensis	4000 - 12000	9 - 15
P. wawrae	5000	7 - 15

LITERATURE CITED

Alejandro, G. J. D., Evangelista, C. G., Banag, C. I., Getuiza, L. K. M., Liberato, E. T., Punsalan, A. G., & Rosales, J. C. (2008). Phylogenetic positions of the tuberous Rubiaceous epiphytes (ant plants) inferred from ITS1, 5.8s gene and ITS2 region (nrDNA) sequence data. *The Philippine BIOTA*, *41*(1), 17-29.

Alexander, P. J., Rajanikanth, G., Bacon, C. D., & Bailey, C. D. (2007). Recovery of plant DNA using a reciprocating saw and silica-based columns. *Molecular Ecology Notes*, *7*(1), 5–9.

Álvarez, I., & Wendel, J. F. (2003). Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution*, *29*(3), 417–434.

Angert, A. L. (2009). The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proceedings of the National Academy of Sciences of the United States of America*, *106 Suppl 2*, 19693–19698.

Arribas, P., Velasco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., … Bilton, D. T. (2012). Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, *39*(5), 984–994.

Baldwin, B. G., Kyhos, D. W., Dvorak, J., & Carr, G. D. (1991). Chloroplast DNA evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). *Proceedings of the National Academy of Sciences of the United States of America*, *88*(5), 1840–1843.

Baldwin, B. G. (1992).. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the compositae. *Mol Phylogenet Evol, 1*(1), 3-16.

Baldwin, B. G., & Markos, S. (1998). Phylogenetic utility of the external transcribed spacer (ETS) of 18S-26S rDNA: congruence of ETS and ITS trees of Calycadenia (Compositae). *Molecular Phylogenetics and Evolution*, *10*(3), 449–463.

Bandelt, H., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution, 16*(1), 37–48.

Barrabé, L., Buerki, S., Mouly, A., Davis, A. P., Munzinger, J., & Maggia, L. (2012). Delimitation of the genus Margaritopsis (Rubiaceae) in the Asian, Australasian and Pacific region, based on molecular phylogenetic inference and morphology. *Taxon*, *61*(6), 1251–1268.

Barrabé, L., Maggia, L., Pillon, Y., Rigault, F., Mouly, A., Davis, A. P., & Buerki, S. (2014). New Caledonian lineages of Psychotria (Rubiaceae) reveal different evolutionary histories and the largest documented plant radiation for the archipelago. *Molecular Phylogenetics and Evolution*, *71*(1), 15–35.

Bennett, G. M., & O'Grady, P. M. (2013). Historical biogeography and ecological opportunity in the adaptive radiation of native Hawaiian leafhoppers (Cicadellidae: Nesophrosyne). *Journal of Biogeography*, *40*(8), 1512–1523.

Bremer, B., Jansen, R. K., Oxelman, B., Backlund, M., Lantz, H., and Kim, K.J. (1999). More characters or more taxa for a robust phylogeny— case study from the coffee family (Rubiaceae). *Systematic Biology, 48*, 413–435.

Bremer, B., Bremer, K., Heidari, N., Erixon, P., Olmstead, R. G., Anderberg, A. a., … Barkhordarian, E. (2002). Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. *Molecular Phylogenetics and Evolution*, *24*(2), 274–301.

Bremer, B., & Eriksson, T. (2009). Time Tree of Rubiaceae: Phylogeny and Dating the Family, Subfamilies, and Tribes. *International Journal of Plant Sciences, 170*(6), 766-793

Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, *27*, 597–623.

Clague D. A., Dalrymple, G. B. (1987). Tectonics, geochronology and origin of the Hawaiian-Emperor volcanic chain. In: Volcanism in Hawaii (eds Decker RW, Wright TL, Stauffer PH), pp. 1–54. U*S Geological Survey Professional Paper*, 1350. US Government.

Canfield, J. E. (1981). Palau: diversity and status of the native vegetation of a unique Pacific Island ecosystem. *Newsletter of the Hawaiian Bot. Soc., 20*, 14–20.

Carson, H. L., Clague, D. A. (1995). Geology and biogeography of the Hawaiian Islands. In: Hawaiian Biogeography: Evolution in a Hotspot Archipelago (eds Wagner W, Funk V), 14–29. *Smithsonian Institution Press*, Washington, DC.

China Plant BOL Group, Li, D. Z., Gao, L. M., Li, H. T., Wang, H., Ge, X. J., et al. (2011). Comparative analysis of a large dataset indicates that internal transcribed spacer (ITS) should be incorporated into the core barcode for seed plants. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 19641–19646.

Clegg, M. T., Gaut, B. S., Learn, G. H., & Morton, B. R. (1994). Rates and patterns of chloroplast DNA evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *91*(15), 6795–6801.

Clement, M., Posada, D. & Crandall, K. (2000). TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, *9*(10), 1657-1660.

Clement, M., Snell, Q., Walker, P., Posada, D., & Crandall, K. (2002). TCS: Estimating gene genealogies. Parallel and Distributed Processing Symposium, *International Proceedings, 2*, 184.

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nat Meth*, *9*(8), 772.

Devey, C. W. et al. (1997). The Foundation Seamount Chain: a first survey and sampling. *Mar. Geol., 137*, 191–200.

Dixon, C. J., Kapralov, M. V., & Filatov, D. A. (2011). Gene flow and species cohesion following the spread of Schiedea globosa (Caryophyllaceae) across the Hawaiian Islands. *Journal of Evolutionary Biology*, *24*(1), 1–11.

Dong, L. (2013). *Phylogenetic Studies Of New World species in the plant genus Psychotria (Rubiaceae)* (Doctoral dissertation).

Dong, W., Liu, J., Yu, J., Wang, L., & Zhou, S. (2012). Highly Variable Chloroplast Markers for Evaluating Plant Phylogeny at Low Taxonomic Levels and for DNA Barcoding. *PLoS ONE*, *7*(4), e35071.

Drummond, A.J., Suchard, M.A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*(8), 1969–1973.

Edgar, R. C. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, *32*(5), 1792–1797.

Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(January), 129–151.

Emerson, B.C. (2002). Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Mol Ecol*, *11*, 951–966.

Farris, J. S., Kallersjo, M., Kluge, a G., & Bult, C. (1995). Testing significance of incongruence. *Cladistics*, *10*, 315-319.

Felsenstein, J. (2004). Inferring phylogenies. *Sinauer Associates*, Sunderland, Massachusetts.

Fleischer, R. C., McIntosh, C. E., & Tarr, C. L. (1998). Evolution on a volcanic conveyor belt: using Phylogeographic reconstructions and K-Ar-based ages of the Hawaiian islands to estimate molecular evolution rates. *Molecular Ecology*, *7*, 533–545.

Florin, R. (1963). The distribution of conifer and taxad genera in time and space: Acta Horti Bergiani, *20*, 121-312.

Fosberg, F. R. (1962). Miscellaneous notes on Hawaiian plants—3. Occas. Pap. *Bernice P. Bishop Mus*, *23*, 42–44.

Fosberg, F. R. (1964). Studies in Pacific Rubiaceae: *V. Brittonia*, *16*, 255– 271.

Frankham R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity*, 78, 311–327.

Fritz, S. A., Jønsson, K. a., Fjeldså, J., & Rahbek, C. (2012). Diversification and biogeographic patterns in four island radiations of passerine birds. *Evolution*, *66*(1), 179–190.

Funkhouser, J. G. (1968). The determination of a series of ages of Hawaiian volcanoes by the potassium-argon method, *Pac Sci*, 22(3), 369-372.

Futuyma, D. (2013). Evolution. *Sinauer Associates*, Sunderland, Massachusetts.

Gaston, K. J. (2003). The Structure and Dynamics of Geographic Ranges. *Oxford University Press*, Oxford, UK.

Gillespie, R. G. & Baldwin, B. G. (2010). Island biogeography of remote archipelagos. The theory of island biogeography revisited (ed. by J.B. Losos and R.E. Ricklefs), pp. 358–387. *Princeton University Press*, Princeton, NJ.

Givnish, T. J., Millam, K. C., Mast, A. R., Paterson, T. B., Theim, T. J., Hipp, A. L., … Sytsma, K. J. (2009). Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings. Biological Sciences / The Royal Society*, *276*(1656), 407–416.

Gove, A. D., Fitzpatrick, M. C., Majer, J. D., & Dunn, R. R. (2009). Dispersal traits linked to range size through range location, not dispersal ability, in Western Australian angiosperms. *Global Ecology and Biogeography*, *18*(5), 596–606.

Gray, A., (1858). Notes upon some Rubiaceae collected in the United States South Sea Exploring Expedition under Captain Wilkes, with characters of new species, etc. *Proc. Amer. Acad. Arts*, *4*, 33–50.

Graybeal, A. (1998). Is it better to add taxa or characters to a difficult phylogenetic problem. *Syst. Biol., 47*, 9–17.

Gutiérrez-Rodríguez, C., Ornelas, J. F., & Rodríguez-Gómez, F. (2011). Chloroplast DNA phylogeography of a distylous shrub (Palicourea padifolia, Rubiaceae) reveals past fragmentation and demographic expansion in Mexican cloud forests. *Molecular Phylogenetics and Evolution*, *61*(3), 603–615.

Hernández, P.A., Graham, C. H., Master, L. L. & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, *29*(June), 773–785.

Hijmans, R. J., Guarino, L., & Mathur, P. (2004). DIVA-GIS. Version 7.5. A geographic information system for the analysis of species distribution data.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978.

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–218.

Huelsenbeck, J.P. (1991). When are fossils better than extant taxa in phylogenetic analysis? *Syst Zool, 40*, 458–69.

Jaffre´, T., Morat, P., Veillon, J.-M. & MacKee, H. S. (1987). Changements dans la vegetation de la Nouvelle-Cale ´onie au cours du Tertiaire: la vegetation et la flore des roches ultrabasiques. *Bull. Mus. Natl. Hist., Paris, Se ´r.4, Sect. B, Adansonia, 9*, 365–391.

Jang, Y., Won, Y.J., Choe. J.C. (2009). Convergent and divergent patterns of morphological differentiation provide more evidence for reproductive character displacement in a wood cricket Gryllus fultoni (Orthoptera: Gryllidae). *BMC Evol Bi*ol, *9*, 27.

Jetz, W., Sekercioglu, C. H., & Watson, J. E. (2008). Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology*, *22*(1), 110-119.

Jones, K. E., Sechrest, W., & Gittleman, J. L. (2005). Age and area revisited: identifying global patterns and implications for conservation. Pages 142–165 in A. Purvis, J. L. Gittleman, and T. Brooks, eds. Phylogeny and conservation. Cambridge University Press, Cambridge.

Kapralov, M. V., Votintseva, A. A., & Filatov, D. A. (2013). Molecular adaptation during a rapid adaptive radiation. *Molecular Biology and Evolution*, *30*(5), 1051–1059.

Kårehed, J., Groeninckx, I., Dessein, S., Motley, T. J., & Bremer, B. (2008). The phylogenetic utility of chloroplast and nuclear DNA markers and the phylogeny of the Rubiaceae tribe Spermacoceae. *Molecular Phylogenetics and Evolution*, *49*(3), 843–866.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., … Drummond, A. (2012). Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*(12), 1647–1649.

Kelchner, S. A. (2002). Group II introns as phylogenetic tools: Structure, function, and evolutionary constraints. *American Journal of Botany*, *89*(10), 1651–1669.

Kozak, K. H., & Wiens, J. J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, *13*(11), 1378–1389.

Kress, W.J., Urdack, K.J., Zimmer, E.A., Weight, L.A., & Janzen, D.H. (2005). Use of DNA barcodes to identify flowering plants. *Proceedings of the NAtional Academy of Science*, *102*, 8369-8374.

Lester, S. E., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology Letters*, *10*(8), 745–758.

Logacheva, M. D., Valiejo-Roman, C. M., Degtjareva, G. V., Stratton, J. M., Downie, S. R., Samigullin, T. H., & Pimenov, M. G. (2010). A comparison of nrDNA ITS and ETS loci for phylogenetic inference in the Umbelliferae: An example from tribe Tordylieae. *Molecular Phylogenetics and Evolution*, *57*, 471-476.

Matzke, N. J., (2013). BioGeoBEARS: BioGeography with Bayesian (and Likelihood). Evolutionary Analysis in R Scripts. Release R package version 0.2.1.

Matzke, N. J., (2014). Model selection in historical biogeography reveals that founder- event speciation is a crucial process in island clades. *Systematic Biology, 63*, 951–970.

MacArthur, R.H. & Wilson, E.O. (1967). The theory of island biogeography. *Princeton University Press*, Princeton, NJ.

McDougall, I. (1964). Potassium-argon ages from lavas of the Hawaiian Islands. *Geol. Soc. Am. Bull*, *75*, 107-128.

Mortimer, N. (2004). New Zealand's geological foundations. *Gondwana Research, 7*, 261–272.

Murray, B. R., & Hose, G. C. (2005). Life-history and ecological correlates of decline and extinction in the endemic Australian frog fauna. *Austral Ecology*, *30*, 564–571.

Naidoo, K., Steenkamp, E. T., Coetzee, M. P. A., Wingfield, M. J., & Wingfield, B. D. (2013). Concerted Evolution in the Ribosomal RNA Cistron. *PLoS ONE*, *8*(3).

Neall, V. E., & Trewick, S. A. (2008). The age and origin of the Pacific islands: a geological overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1508), 3293–3308.

Nepokroeff, M., Bremer, B., & Sytsma, K. J. (1999). Reorganization of the genus Psychotria and Tribe Psychotrieae (Rubiaceae) inferred from ITS and rbcL sequence data. *Systematic Botany*, *24*(1), 22.

Nepokroeff, M., Sytsma, K. J., Wagner, W. L., & Zimmer, E. A. (2003). Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory tree genus Psychotria (Rubiaceae): a comparison of parsimony and likelihood approaches. *Systematic Biology*, *52*(6), 820–838.

Palmer, J. D. (1985). Chloroplast DNA and molecular phylogeny. *BioEssays*, *2*(6), 263–267.

Patwardhan, A., Ray, S., & Roy, A. (2014). Phylogenetics & Evolutionary Biology Molecular Markers in Phylogenetic Studies-A Review. *Journal of Phylogenetics & Evolutionary Biology*, *2*(2).

Poe, S., and Swofford, D. L. (1999). Taxon sampling revisited. *Nature, 398*, 299–300.

Paul, J. R., Morton, C., Taylor, C. M., & Tonsor, S. J. (2009). Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant genus Psychotria (Rubiaceae). *The American Naturalist*, *173*(2), 188–199.

Phillips, S.J., Dudík, M., & Schapire, R. (2004). A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First …*, 655–662.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3-4), 231–259.

Pigot, A. L., Owens, I. P. F., & Orme, C. D. L. (2012). Speciation and extinction drive the appearance of directional range size evolution in phylogenies and the fossil record. *PLoS Biology*, *10*(2).

Pillon, Y., Johansen, J., Sakishima, T., Chamala, S., Barbazuk, W. B., Roalson, E. H., … Stacy, E. a. (2013). Potential use of low-copy nuclear genes in DNA barcoding: a comparison with plastid genes in two Hawaiian plant radiations. *BMC Evolutionary Biology*, *13*(1), 35.

Poczai, P., & Hyvönen, J. (2010). Nuclear ribosomal spacer regions in plant phylogenetics: Problems and prospects. *Molecular Biology Reports*, *37*(4), 1897–1912.

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, *3*(4), 349–361.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raxworthy, C. J., Martinez-Meyer, E., Horning, N., Nussbaum, R. A., Schneider, G. E., Ortega-Huerta, M. A, & Townsend Peterson, a. (2003). Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, *426*(6968), 837–841.

Razafimandimbison, S. G., Taylor, C. M., Wikström, N., Pailler, T., Khodabandeh, A., & Bremer, B. (2014). Phylogeny and generic limits in the sister tribes Psychotrieae and Palicoureeae (Rubiaceae): Evolution of schizocarps in Psychotria and origins of bacterial leaf nodules of the Malagasy species. *American Journal of Botany*, *101*(7), 1102–1126.

Ree, R. H., & Smith, S. a. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*(1), 4–14.

Ricklefs, R. E. (1987). Community Diversity: Relative Roles of Local and Regional Processes. *Science*, *235*(4785), 167–171.

Ricklefs, R. E., & Bermingham, E. (2002). The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography*, *11*(5), 353–361.

Ricklefs, R. E. (2008). Disintegration of the ecological community. *The American Naturalist*, *172*(6), 741–750.

Ricklefs, R. E. (2012). Naturalists, Natural History, and the Nature of Biological Diversity. *The American Naturalist*, *179*(4), 423–435.

Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, *1*, 319–329.

Rolland, J., Cadotte, M. W., Davies, J., Devictor, V., Lavergne, S., Mouquet, N., … Morlon, H. (2012). Using phylogenies in conservation: new perspectives. *Biology Letters*, *8*(5), 692–694.

Ronquist, F., Huelsenbeck, J.P., (2003). MrBAyes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*, 1572–1574.

Ruhsam, M., Rai, H. S., Mathews, S., Ross, T. G., Graham, S. W., Raubeson, L. A., … Hollingsworth, P. M. (2015). Does complete plastid genome sequencing improve species discrimination and phylogenetic resolution in Araucaria? *Molecular Ecology Resources*, n/a–n/a.

Sang, T., Crawford, D. J., & Stuessy, T. F.. (1995). Documentation of reticulate evolution in peonies (Paeonia) using internal transcribed spacer sequences of nuclear ribosomal DNA:Implications for biogeography and concerted evolution. *Proc. Natl. Acad. Sci. USA, 92*, 6813–6817.

Sang, T. (2002). Utility of low-copy nuclear gene sequences in plant phylogenetics. *Critical Reviews in Biochemistry and Molecular Biology*, *37*(3), 121–147.

Schluter, D. (2000). Ecological Character Displacement in Adaptive Radiation. *The American Naturalist*, *156*(s4), S4–S16.

Sedio, B. E., Paul, J. R., Taylor, C. M., & Dick, C. W. (2013). Fine-scale niche structure of Neotropical forests reflects a legacy of the Great American Biotic Interchange. *Nature Communications*, *4*, 2317.

Sheth, S. N., & Angert, A. L. (2014). The Evolution of Environmental Tolerance and Range Size: a Comparison of Geographically Restricted and Widespread Mimulus. *Evolution*, *68*(10), 2917–2931.

Slayter, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, *16*(8), 1104–1114.

Sohmer, S. (1977). *Psychotria* L. (Rubiaceae) in the Hawaiian islands. *Lyonia*, *1*(3), 103–186.

Sohmer, S. (1978). Morphological variation and its taxonomic and evolutionary significance in the Hawaiian Psychotria (Rubiaceae). *Brittonia*, 30, 256–264.

Sohmer, S., & Davis, A. P. (2007). The Genus *Psychotria (Rubiaceae)* in the Philippine Archipelago. Fort Worth, Texas: Botanical Research institute of Texas.

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*(9), 1312–1313.

Swaegers, J., Janssens, S. B., Ferreira, S., Watts, P. C., Mergeay, J., McPeek, M. a., & Stoks, R. (2014). Ecological and evolutionary drivers of range size in Coenagrion damselflies. *Journal of Evolutionary Biology*, *27*(11), 2386–2395.

Swofford, D. L. (2003). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. *Sinauer Associates*, Sunderland, Massachusetts.

Taylor, C. M. (1996). Overview of the Psychotrieae (Rubiaceae) in the Neotropics. *Opera Botanica Belgica*, *7*, 261–270.

Templeton, A. R., Crandall, K. A, & Sing, C. F. (1992). A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics*, *132*, 619–633.

Tennessen, J.A., Akey, J.M. (2011). Parallel Adaptive Divergence among Geographically Diverse Human Populations. *PLoS Genet, 7*(6), e1002127.

Thomson, F. J., Moles, A. T., Auld, T. D., and Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol. 99*, 1299–1307.

Title, P. O., & Burns, K. J. (2015). Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. *Ecology Letters*.

Turner, B., Munzinger, J., Duangjai, S., Temsch, E. M., Stockenhuber, R., Barfuss, M. H. J., … Samuel, R. (2013). Molecular phylogenetics of New Caledonian Diospyros (Ebenaceae) using plastid and nuclear markers. *Molecular Phylogenetics and Evolution*, *69*(3), 740–763.

Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography*, *33*(3), 607–611.

Werner, R., Hoernle, K., van der Boogaard, P., Ranero, C., von Huene, R. & Korich, D. (1999). A drowned 14 m.y.-old Galapagos archipelago off the coast of Costa Rica: implications for tectonic and evolutionary models. *Geology, 27*, 499–502.

Wheelwright, N. T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, *66*, 808–818.

Whittaker, R. J., Triantis, K. A. & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, *35*, 977–94.

Wiens, J. J. (2003). Missing data, incomplete taxa, and phylogenetic accuracy. *Syst Biol, 52*, 528–38.

Wiens, J. J. (2006) Missing data and the design of phylogenetic analyses. *J. Biomed. Inform., 39*, 34–42.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., … Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*(10), 1310–1324.

Willis, J. C. (1922). Age and area: a study in geographical distribution and origin of species. *Cambridge University Press*, Cambridge, UK.

Wilson, E. O. (1961). The nature of the taxon cycle in the Melanesian ant fauna. American Naturalist, *95*, 169-193.

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology and Evolution*, *28*(4), 199–204.